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Overview of habitat history in subtropical oceanic island summit ecosystems

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Abstract

Summit ecosystems of oceanic islands constitute one of the most ephemeral and isolated ecosystems existing, harboring specific features that confer on their biota an outstanding distinctness. Summits are short-lived entities, being the last ecosystems to be constructed during the growth of the new oceanic island, and the first to vanish due either to island subsidence, island erosion, or both. Whereas their geological emergence/disappearance is controlled by the volcanic/erosion activity, Pleistocene glaciations in the past million years, by forcing the altitudinal shift of the timberline, have also likely created or destroyed summit ecosystems, enabling the appearance of alpine ecosystems during glacial maxima where they were not present in interglacial periods and vice versa.

On the other hand, summit ecosystems constitute islands within islands, being more isolated from climatically similar ecosystems than the coastlines of the islands containing them. Thus summit biota, frequently displaying a high endemicity, may originate either through dispersal from other close summit ecosystems during peak periods, or from the colonization of the summits and later evolution to the new conditions from mid-altitude species of the same island. Conversely, if peak periods are absent, the disappearance of summit ecosystems implies the extinction or extirpation of their constitutive species. Current summit species have likely occupied a much larger area during glacial periods. Thus the summits may be classified as climatic refuges. This is especially the case if glacial periods were associated with much drier conditions on oceanic islands as is the case on continents.

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Introduction

Mountain summit ecosystems are a significant component of many tropical and subtropical islands. They harbor specific characteristics that confer on their biota an outstanding distinctness and constitute one of the most ephemeral and isolated kinds of ecosystems (Steinbauer et al., 2012, 2013). In spite of their significance, these ecosystems are still understudied, and even a basic understanding of the processes underlying the distribution and abundance of plant and animal communities in their biota remains elusive.

In this review, we focus on the processes, both geological and climatic, that explain the spatial and temporal dynamics of mountain summit ecosystems in (sub)tropical islands and explore how these dynamics may influence species diversity and affect the balance between speciation and extinction in this unique biota. Before doing so, we first consider the concept of timberline, which provides a useful framework within which mountain summit ecosystems can be defined and characterized. We then explore the concept of "island ontogeny," with a description of the different life phases of oceanic islands of volcanic origin. Finally, we consider the contribution that analyses of geological and climatic events and of the physical attributes of islands are making to the understanding of the origin and evolution of species diversity.

Definition of Summit Ecosystems: the Concept of Timberline

Altitudinal timberlines or treelines mark the upward replacement of tree-dominated communities by non-tree-dominated communities along an elevational gradient on mountains (Leuschner, 1996). They represent (together with latitudinal timberlines) one of the more striking examples of vegetation discontinuity in nature and have been intensively studied in subtropical and tropical zones of continents or continental islands (Troll, 1959, 1968), but only rarely in subtropical and tropical oceanic islands (Leuschner, 1996) (Table 1).

In contrast with tropical latitudes where a timberline is harder to define due to the high precipitation falling in the islands' summits, the arid subtropical islands' summits above the trade wind–influenced zone typically display well-defined summit ecosystems above the timberline. Those summit ecosystems are usually dominated by shrubby or herbaceous vegetation, which show a sharp boundary with the forest formations dominating the islands' mid-elevations, which are not able to grow at the summits due to the hydric stress limitation (Höllermann, 1978; Leuschner and Schulte, 1991; Fernández-Palacios et al., 1992).

Leuschner (1996) found that in general oceanic island timberlines are significantly lower than the timberlines of the nearest continental chains located at comparable latitudes. He postulated different reasons for explaining such differences: (*a*) the youth of the summits of recent oceanic islands, which are still being constructed (e.g., what happens in Pico [Azores], Fogo [Cape Verde], Mauna Loa [Big Island], Grand Comoro or Piton de la Fournaise in Réunion); (*b*) the isolation-based species impoverishment of oceanic islands, which could restrict the in situ availability of the tree species exploiting such harder climatic conditions on the continents (the case of Maui and Hawaii summits); (*c*) the small mountain mass effect, which influences the vertical temperature gradient in summits; (*d*) the summit drought on trade wind exposed island peaks; (*e*) the strong

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TABLE 1

Geographical data of selected subtropical islands summits (various sources).

Island	Big Island (Hawai'i)	Maui (Hawai'i)	Tahiti (Society)	Grande Comoro (Comoros)	Réunion (Mascarenes)	Tenerife (Canaries)	La Palma (Canaries)	Fogo (Cape Verde)
Highest Peak (m) + constructive ↑ vs. destructive ↓ dynamic	Mauna Kea ↑ (4205) Mauna Loa ↑ (4169)	Haleakala ↑ (3055) Pu'u Kukui ↓ (1764)	Orohena ↓ (2241) Mount Ronui ↑ (1332)	Khartala ↑ (2361)	Piton des Neiges ↓ (3069) Piton de la Fournaise ↑ (2632)	Pico del Teide ↑ (3718)	Taburiente ↓ (2425) Cumbre Vieja ↑ (1950)	Pico de Fogo ↑ (2829)
Summit last eruption	MK: 4.6 ka BP ML: AD 1984	Haleakala A.D. 1790	?	A.D. 2005	Piton des Neiges 70 ka BP, Piton de la Fournaise 2010	A.D. 1798	Taburiente: 0.4 Ma BP/ Cumbre Vieja A.D. 1949	A.D. 1995
Continental isolation (km)	3900	3900	5900	300	700	300	400	700
Latitude (°)	20 N	21 N	18 S	12 S	21 S	28 N	28 N	15 N
Approx. timberline (m)	2900	2500	2000	2200	2000	2300	2000	2000 ?
Area above timberline (km^2)	1745	123	1.25	?	170	145	15	?
Island's area above timberline (%)	16.7	6.50	—	?	6.77	7.07	2.02	?
Summit ecosystem (sensu Leuschner, 1996, slightly modified)	Dry open scrub (2900–3200) + Dry open dwarf scrub & grass semidesert (3200–3900) + alpine stony desert with lichens & mosses (3900–4200)	Dry open scrub (2900–3200	Subalpine forest (2000–2250)	Dry ericaceous scrub (2200–2350) dominated by *Erica comorensis*	Dry ericaceous scrub, open dwarf scrub, and semidesert dominated by *Erica* spp., *Stoebe passerinoides, Phylica nitida,* and *Psiadia* spp. (2200–3000)	Dry leguminous scrub (2000–3000) dominated by *Spartocytisus supranubius* + semidesert & desert with mosses and lichens (3000–3700)	Dry leguminous scrub (2000–2400) dominated by *Adenocarpus viscosus*	Semidesert

winds affecting exposed island summits; or (*f*) the anthropogenic disturbance, which likely may have extirpated tree species able to grow above the present timberline (the case of *Juniperus cedrus* in La Palma and Tenerife, the Canaries) (Nogales et al., 2014).

Here, we postulate a further reason: the rare and ephemeral character of oceanic island summits, which avoid evolutionary opportunities for producing endemic treeline species. To explore this last reason in greater depth, we first need to revisit the oceanic island ontogeny concept (Stuessy, 2007; Whittaker et al., 2007, 2008).

The Concept of Island Ontogeny As Applied to Oceanic Islands

Starting with Alfred Russel Wallace (1902), real islands have been classified in three different categories: continental islands, continental fragments or micro-continents, and oceanic or volcanic islands (Whittaker and Fernández-Palacios, 2007). Oceanic islands share a volcanic origin and their more important biogeographical feature is their emergence from the sea surface devoid of life, after the accumulation of lavas during millions of years of volcanic activity. They have a highly variable life span, ranging from a couple of days (Sabrina, Azores, 1811) to tens of millions of years (e.g., Selvagem Grande, Madeira 27 m.y.) and different origins, such as volcanic arches developed above subduction zones (Lesser Antilles), volcanic structures related to mid-oceanic ridges (Azores), intra-plate mantle plumes (Madeira, Canaries), or yet unknown (Cape Verde). During their construction, oceanic islands may reach considerable altitudes (Hawaii, 4200 m altitude) and areas (Iceland, 100,000 km^2), although they are usually small (Fernández-Palacios and Martín Esquivel, 2001; Fernández-Palacios, 2004).

Recently Whittaker et al. (2007, 2008) have refreshed the idea that hot spot oceanic islands, as opposed to the stable continental islands and fragments, function like living beings that are born, and then grow, age, and eventually disappear under the sea level with time (Ziegler, 2002), incorporating the role of island age in the parameters controlling the species richness that a given island can harbor. These authors propose the use of the term *island ontogeny* (term coined by Stuessy, 2007) for the set of changes in geographic and biogeographic parameters that an oceanic island undergoes during its life.

The Different Life Phases of an Oceanic Island

The life of an oceanic island, if not affected by the growth of coral reefs (Fernández-Palacios and Whittaker, 2011), is constituted by a continuously changing environment from its birth on the ocean floor to its final disappearance under the sea surface (Fig. 1). This continuum of development can be easily described for simplification purposes by six different ontogeny phases as follows: (*a*) birth and submarine construction phase, (*b*) emersion and aerial construction phase, (*c*) erosion and landslides phase, (*d*) basal plain phase, (*e*) terminal disappearance phase, and (*f*) cut-summit seamount (guyot) phase. During the first and last phases, the island is actually a seamount. The first phase is longer lasting and is often not concluded, leading to seamounts that will never reach the sea surface. These never-emerged-seamounts do not show a flat summit, in contrast to guyots (emerged and later eroded to the sea-level island). During the second phase, which can be of a relatively short duration, the island reaches its maximal area and altitude. Later, destructive processes, such as erosion, gravitational landslides, or subsidence, begin to work and they will progressively dismantle the island, first to a dramatic topography with huge valleys (phase c), and later to a flatter landscape with increasingly eroded mountain peaks (phase d), which will slowly disappear under the sea surface (phase e). Once under the sea surface, erosion is less active and the former island, now seamount, will possess a flat summit (guyot), an unmistakable feature of its former insular nature (phase f), and will last as seamount for extended periods of time. Some of these seamounts, in particular those that are little affected by subsidence due to oceanic floor cooling, may become periodically emergent during periods of low sea levels (glacial transgressions).

In regions where the islands are surrounded by warm waters, the development of coral reefs may first ring the subsiding island and eventually will form atolls, when the island disappears below sea level (Ziegler, 2002), that may last several m.y. before disappearing through subduction beneath the continental crust or when the atolls, due to the plate movement, reach the Darwin point, that is, the latitude at which the low sea temperature inhibits the further growth of corals (Grigg, 1982).

Within this context, our aim in the present contribution is to go deeper in the habitat history of summit ecosystem on oceanic islands, stressing the role of geological and climatic events in their emergence, altitudinal shift, or disappearance, and in the consequences of such circumstances on the evolution and extinction of their unique biota. Whereas geological events will not change the altitudinal location of the timberline, they will affect strongly

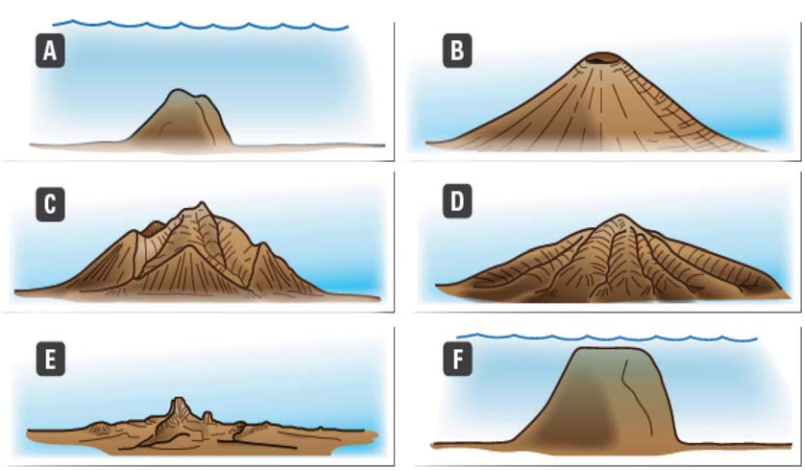

FIGURE 1. Different life phases of a hot-spot originated oceanic island. See text for the meaning of the different phases recognized (Source: Fernández-Palacios and Whittaker, 2010).

(either increasing or decreasing) the portion of the island existing above it. Conversely, climatic events will affect both the island area and island altitude (through the shift of the sea level), affecting as well the altitudinal location of the timberline (and the line of perpetual snows if existing). Finally, both geological and climatic events affecting oceanic islands have different rhythms and tempos, the former usually lasting millions of years, the latter lasting millennia or tens of millennia.

Geologic Events Affecting Summit Ecosystems

From a paleoecological and a paleobiogeographical point of view, oceanic island summits should be considered as very rare and ephemeral ecosystems. They never occupy large areas (at least in comparison with other insular ecosystems), nor last long, as they constitute either the last part of the emerging oceanic island being constructed, or the first part of the vanishing island being eroded and/or subsiding. On the one hand, there are young summits that are being constructed by the accumulation of volcanic material above the timberline (*geological summit emergence*) and are usually found on young, recently formed islands still under construction. These young, growing summits are subject to recurrent volcanic activity, explosions, lava flows, and thus experience several unsynchronized primary succession cycles, implying a high dynamism that creates many opportunities for species colonization and establishment. Their vegetation is far from equilibrium, usually scarce, and distributed in a mosaic pattern, with a predominance of high altitude stone deserts. Examples include Mauna Kea, Mauna Loa, and Hualalai (Island of Hawai'i), Haleakala (Maui), Pico (Azores), Teide Peak (Tenerife), Pico do Fogo (Fogo), Karthala (Grand Comore), or Piton de la Fournaise (Réunion).

On the other hand, there are old summits on islands predominantly subject to erosion or subsidence. The existence of a summit above the timberline on an old volcanic island testifies to the higher altitude of the island in the past, meaning that it has already experienced a considerable summit loss in terms of both area and altitude. These simultaneously constitute remnants of summit ecosystems that are vanishing and that are the biotic source for more recently formed summits that, if dispersal opportunities exist, will take over after they vanish. These vanishing summits have likely been prone to biodiversity losses, and their present biota is only a fraction of their original biota. Furthermore, these summit ecosystems are much less dynamic than the former type, usually holding mature communities in the absence of primary succession, and thus fewer opportunities for new colonizing species due to niche preemption by established species. Examples of vanishing summits include Pico Riuvo (Madeira), Roque Nublo (Gran Canaria), Taburiente (La Palma), Piton des Neiges (Réunion), or Orohena (Tahiti).

When a newly emerged island achieves a summit before the disappearance (due to erosion or subsidence) of the summit of its older neighboring island, a transfer of summit pre-adapted species from the older to the younger island is possible (Fig. 2), the likelihood depending on the dispersal context (i.e., dispersal agents, such as wind intensity and direction, and dispersal abilities of the species involved). This case has been designated as a *peak period* (sensu Price and Clague, 2002), which enables the survival of an old species on a new island. The age of these surviving species can thus predate the age of the island where they are today distributed. These neo-endemic species, present on a different summit or island from that which they originated (which are now sunken), can be called old neo-endemics, in contrast to young neo-endemics. Both of these contrast with species present exclusively on the islands today that were distributed on continents in the past, for instance, the Macaronesian laurel-forest tree species.

In Hawaii, although not frequent, this phenomenon does exist (for instance, in *Drosophila-Scaptomyza* fruit flies), which represent a "Pre-Kauai signal in the present Hawaiian biota" (Price and Clague, 2002) in allusion to the oldest, still high, Hawaiian island: Kauai. The endemic genus *Monimia* on the Mascarenes provides another interesting example of an island lineage being much older than the islands on which it presently occurs (Renner et al., 2010).

In some volcanic islands, such as La Palma (Taburiente–Cumbre Vieja), Maui (Pu'u Kukui–Haleakala), Tahiti (Mount Orohena–Mount Ronui), or Réunion (Piton des Neiges–Piton de la Fournaise), old vanishing summits can co-occur with new emerging summits, usually separated by saddle valleys. Here we may expect a transfer of summit species from the older summit to the younger summit if conditions permit. Following Price and Clague (2002) terminology, this phenomenon could be called a within-island peak period.

The Ephemeral Character of the Oceanic Island Summits

How much time will pass between the emersion of a summit above the timberline and its disappearance below it? In other

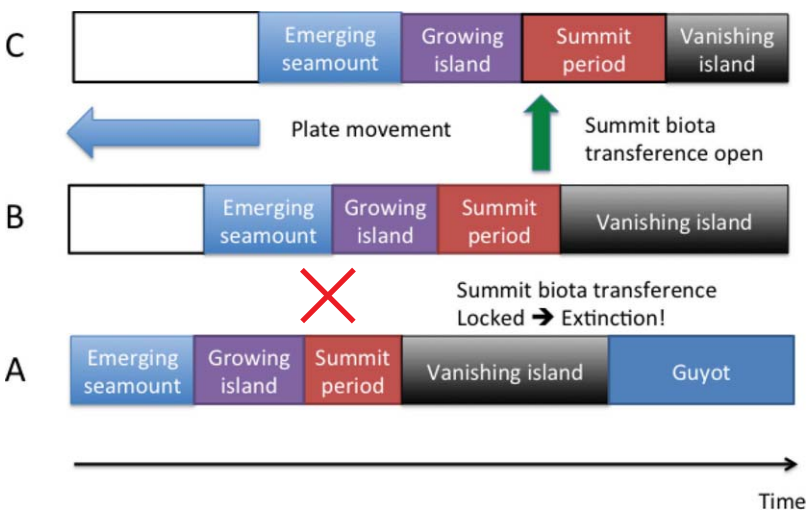

FIGURE 2. Inexistence of an A–B peak period implying no summit biota transference possible and thus extinction, versus B–C peak period implying summit biota transference. A, B, and C are different islands from a given hot-spot archipelago.

words, how long does a summit ecosystem last on a given tropical/subtropical island? To a big degree, this issue will depend on whether island subsidence occurs. In oceanic archipelagos where the oceanic crust is old and rigid enough to prevent island subsidence, as happens for instance in the Canaries (Carracedo, 2011), summits can last longer and will disappear only due to erosion processes. For instance, El Hierro, the westernmost and youngest (1.1 m.y.) of the main Canary Islands, has an altitude of 1501 m. Although still below the timberline (which occurs at 2000–2300 m a.s.l. in the Canaries), it is likely that it will achieve a summit ecosystem above the timberline sometime in the next few thousand years, due to its continued volcanic activity (the most recent being the submarine eruption of La Restinga in 2011). La Palma is a different case, as it is composed of a northern, older half (Taburiente: 2425 m, 1.8 m.y.), and by a southern, younger half (Cumbre Vieja: 1945 m, 0.15 m.y.) separated by a saddle. The island has a summit ecosystem above the timberline in the northern half, which will ultimately disappear due to erosion, and especially due to landslides. Nevertheless, the younger part of the island, volcanically very active (ten eruptions in the last 500 years, most recently by Volcán de Teneguía in 1971), will reach the timberline before Taburiente summit disappears, enabling the transference of summit biota between the two island summits (intra-insular peak period).

Tenerife (3718 m, 11 m.y.) is the highest island of the Canaries, and was even higher in the past (Carracedo, 2011). Volcanic activity of Las Cañadas unified the paleo-islands of Anaga, Teno, and Adeje, beginning 2.5 m.y. ago, and has produced several stratovolcanoes, the last of them, Pico Viejo-Teide, still under construction (the last eruption Volcán de Chinyero being in 1909). Thus, modern Tenerife has had a summit ecosystem for the past 2 m.y., which will likely remain for a long time. Finally, the rest of the islands, although they were high enough to have summit ecosystems (La Gomera, 2600 m [Llanes et al., 2009], Fuerteventura, 3000 m [Stillman, 1999], or Gran Canaria, 2500 m [Pérez Torrado et al., 1995]), lost them due to erosion in the past. From this perspective we may conclude that oceanic islands without significant subsidence may have summit ecosystem continuously for at least 3 m.y.

Conversely, for archipelagos that develop on young oceanic crust, such as Hawai‘i, subsidence is faster and more important than erosion (Carson and Clague, 1995), so that the summit ecosystems vanish comparatively faster (Table 2). For instance, the two Hawai‘i Island summits, Mauna Loa (4169 m, 0.2 m.y.) and Mauna Kea (4206 m, 0.4 m.y.), as well as Haleakala (3060 m, 1.1 m.y.) on Maui, are still under construction and have surpassed the timberline, located here at 2500–2900 m a.s.l. (Leuschner, 1996). Nonetheless, they have already been prone to considerable subsidence, especially Haleakala, which achieved an altitude of 3500 m in the past (Price and Elliott-Fisk, 2004). Moreover, both West Maui (1764 m, 1.3 m.y.) and Molokai (1525 m, 1.76 m.y.) summits, today beneath the timberline, have been prone to subsidence (both having reached altitudes of 3300 m) (Carson and Clague, 1995) and later, as their very dissected landscape show, to extensive erosion. A similar sequence occurred on Oahu and Kauai. From these estimates, we may conclude that summit ecosystems in Hawai‘i, an archipelago strongly affected by island subsidence, may last not much more than 1 m.y.

The Exacerbation of Insularity

From a biogeographical perspective, oceanic insular summits constitute islands within islands, in the sense that they are fewer, smaller, and more isolated than the islands to which they belong. For instance, the Macaronesian region comprises four archipelagos (Azores, Madeira including the Selvagens, the Canaries, and Cape Verde), including 39 islands that together make up an area of slightly more than 15,000 km^2, but only four summits higher than 2000 m composing less than 200 km^2. Furthermore, Macaronesia's largest summit (Las Cañadas del Teide,

TABLE 2

Hawaiian and Canarian summits comparison.

Island/summit	Present altitude (m)	Age (My)	Geological dynamic	Summit above timberline?
Hawai'i archipelago (with subsidence); timberline: 2500–2900 m				
Mauna Loa (Big Island)	4169	0.2	C	Yes
Mauna Kea (Big Island)	4206	0.5	C	Yes
Haleakala (Maui)	3055	1.1	C	Yes
West Maui	1764	1.3	D	No more
Molokai	1515	1.76	D	No more
Oahu	1231	4.0	D	Never
Kauai	1598	5.5	D	No more
Canarian archipelago (without subsidence); timberline: 2000–2300 m				
El Hierro	1501	1.1	C	Not yet reached
Taburiente (La Palma)	2425	3.0	D	Yes
Cumbre Vieja (La Palma)	1949	0.15	C	Not yet reached
Las Cañadas (Tenerife)	3718	2.5	C	Yes
La Gomera	1487	9.2	D	No more
Gran Canaria	1949	15	D	No more
Fuerteventura	807	21	D	No more

Tenerife, 145 km^2) is more than an order of magnitude smaller than its largest island (Tenerife, 2034 km^2), and its isolation from the closest similar ecosystem on the mainland (Djebel Toubkal, in the Atlas Chain, >900 km) is ten times larger than the isolation of the closest island from the continental coast, 96 km among Fuerteventura and the Western Sahara. A similar situation occurs in Polynesia and the Indic Ocean isles (Table 3), not to mention oceanic archipelagos that have no area above the timberline (such as the Galápagos, Juan Fernández, or Marquesas Islands). Thus, oceanic islands' summit ecosystems are the results of an exacerbated insularity, in the sense of comprising fewer, smaller, and more isolated fragments, than the oceanic islands themselves (Fig. 3).

Climatic Events Affecting Summit Ecosystems

Although it is widely accepted that on oceanic islands the temperatures dropped during the Last Glacial Maximum (although not as abruptly as on continents due to the buffer effect of the oceanic masses) (Porter, 1979), our knowledge of the behavior of precipitation is still very scarce. Nevertheless, there is some evidence that high mountain summits were drier than today due to the lower altitude of the trade wind inversion, which would limit the penetration of clouds into this elevation range (Nullet et al., 1998). Thus, as timberline upper limits seem to be controlled by a trade-off of hydric and thermic stresses (Höllermann, 1978), lower temperature and precipitation would promote the downward shift of the forested ecosystems, such as happened with *Acacia koa* and *Sophora chrysophylla* forests in Hawai'i (Nullet et al., 1998).

On this basis, the de novo creation of new summit ecosystems is not necessarily dependent upon the accumulation of volcanic material above the timberline and its disappearance is also not necessarily dependent upon summit erosion or subsidence. A new summit ecosystem may emerge above timberline when the decrease in temperature or precipitation due to glaciation events enables the *climatic or eco-*

TABLE 3

Insularity exacerbation of summit biogeography. Atolls are excluded. As there is no clearly defined timberline in several of the islands or volcanoes used in this table (e.g., Fogo, Grand Comoro, or Mauna Loa), we preferred to use the 2000 m altitude, as an approximation to timberline, for calculating the number of summits and their areas.

	Macaronesia (Azores + Madeira + Canaries + Cape Verde)	Polynesia (Hawai'i + French Polynesia)	Indic Ocean Islands (Seychelles + Mascerenes + Comoros)
No. Islands > 1 km^2	39	49	18
No. Summits (> 2000 m)	4	5	3
	(Pico peak, Taburiente, Teide, and Fogo peak)	(Mauna Kea, Mauna Loa, Hualalai, Haleakala, and Orohena)	(Piton des Neiges, Piton de la Fournaise, and Karthala)
Islands area (km^2)	15,061	20,792	7239
Summits area (km^2)	<200	1868	<200
Largest island (km^2)	Tenerife (2039)	Big Island (10,430)	Réunion (2500)
Largest summit (km^2)	Teide (145)	Mauna Loa (1515)	Piton de la Fournaise (94)
Mainland–island isolation (km)	Fuerteventura–Africa (96)	Big Island–California (ca. 3700)	Grand Comore–Mozambique (300)
Mainland–island summit isolation (km)	Teide–Toubkal, Atlas (900)	Mauna Kea–Sierra Nevada (ca. 4000)	Karthala–Kilimanjaro (1170)

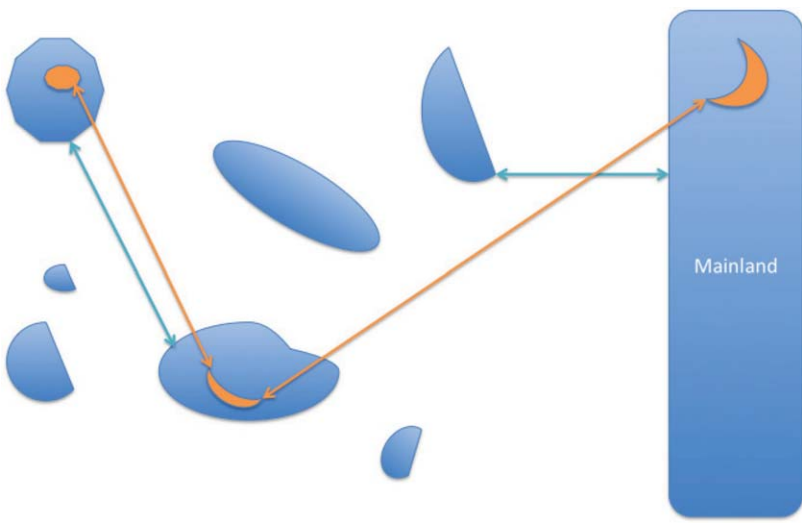

FIGURE 3. Insularity exacerbation of summits compared with island archipelagos: fewer, smaller, and more isolated. Islands and mainland are represented in blue, whereas island and mainland summits are in brown.

logical summit emergence. This is more the result of a decrease of several degrees in the mean annual temperature or amount of annual precipitation, than of an increase in altitude (~130 m) experienced by the island due to the sea level transgressions. Alternatively, the increase in temperatures during interglacial periods results in the ecological disappearance of oceanic islands summit ecosystems.

In very high islands bearing a snowline (the limit of perpetual snow, whose altitude depends on the latitudinal location of the island) above the summit habitat, a third major change in respect to summit habitats' altitudinal distribution will occur. Here both the timberline and the snowline are pushed synchronously upward (during interglacials) or downward (during glacial maxima), so that the summit habitat neither emerged nor vanished, shifting only its altitudinal distribution. This means that the species pool constituting a summit ecosystem traces its climatic requirements through dispersal from either above or below its original altitudinal distribution range. In glaciation maxima, the downward retreat of the timberline (Fig. 4, part a) will leave behind the less vagile species of the forest community, leaving an ecotone community where a mixture of forest and summit shrub species will coexist for a certain time. In contrast, during interglacial periods, the retreat of the perpetual snowline upward (or its eventual disappearance) (Fig. 4, part b) will provide new lifeless terrain to be colonized. In this process the more vagile species will be favored in the colonization of the new terrain, so that the structure and floristic composition of the summit ecosystem can undergo significant ecological changes.

To summarize, the exacerbation of insularity, the ephemeral character, and the climatic dynamism of summit ecosystems may lead to a higher rate of endemism for summit species than that which is characteristic of typical insular biotas (Steinbauer et al., 2012). Thus, many summit vegetation types are dominated by (island or archipelago) endemic, sparsely distributed species, usually well adapted to difficulties of poorly developed soil, as well as the thermic, hydric, and eolian stresses of this particular environment.

Furthermore, summit ecosystems usually exhibit more unique climatic conditions than lower altitude forest ecosystems, due to combinations of hydric and thermic stresses. For instance, we can find similar laurel forests on the three northern Macaronesian archipelagos (Canary Islands, Madeira, Azores) due to similarly high precipitation and moderate temperature conditions, but the summit ecosystems of these archipelagos are completely different. This climatic uniqueness of summit regions strongly influences the formation of regional species pools.

Way-Out versus No-Way-Out Scenarios in Interglacial Events

Depending on the archipelago's geographical configuration, the onset of an interglacial event can give rise to two different scenarios that will contrastingly affect their summit biota. On the one hand, a way-out scenario (Fig. 5, part a) will occur if, after the onset of an interglacial, the disappearance of the above-timberline summit ecosystems due to the increase in temperatures is not absolute throughout the whole archipelago and one or several summit refugia on the highest island(s) still exist (Steinbauer et al., 2013). If intra-island dispersal mechanisms and geographic configuration of the islands permit it (dispersal windows), we may expect only a partial extinction of the summit biota, and these refugia will act as a pre-adapted source of species for the colonization of newly emerging summits, either due to geological events or, more likely, due to the onset of new glaciations.

Conversely, a no-way-out scenario (Fig. 5, part b) will happen if the consequence of an interglacial event is the complete regional disappearance of the summits with no surviving summit refugia (or if they persist, they are beyond the dispersal ability of existing species). Here we predict the complete extinction of the local set of summit species, implying that the colonization of newly emerging summits (either due to volcanic construction or the onset of glaciations) must occur either through colonization of summit pre-adapted continental species (if the archipelago isolation from continental summits is minimal) or more commonly through intra-island summit colonization of new summits by non-pre-adapted, generalistic mid-altitudinal species. In this scenario, an absolutely new set of summit species may arise through in situ evolution of the mid-elevation species that have colonized the emerging summits of a young island. In situ evolution after a "no-way-out" scenario (where earlier summit species vanished during an interglacial) most likely occurs during glacial periods and thus may not be observable from the pattern we find in the present warm stage (Holocene).

Evolutionary Insights: Adaptive Radiation versus Geographic Speciation (Vicariance)

Summit biotas are either the result of dispersal from other high islands that feed them with pre-adapted species during peak periods (cf. Price and Clague, 2002), that is, when windows of dispersal enable summit species to jump from older islands being eroded or subsiding to younger islands under construction, or the product of in situ diversification from a lowland ancestor that colonized and adapted to ecological conditions prevailing on island summits (Trigas et al., 2013). These alternative scenarios can be easily tested using a combination of molecular phylogenetic analyses and information on species distribution and ecology (see, e.g., Knox and Palmer, 1995, and Popp et al., 2008, for continental examples).

A closer phylogenetic relation with a species of the same island occupying a different habitat implies an intra-island sum-

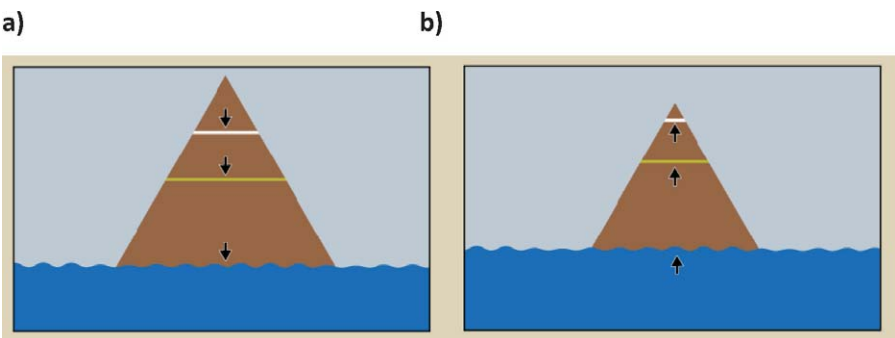

FIGURE 4. (a) Downward retreat of the snowline, timberline, and see level after the onset of a glaciation period, and (b) upward retreat of the snowline, timberline, and see level after the onset of an interglacial period.

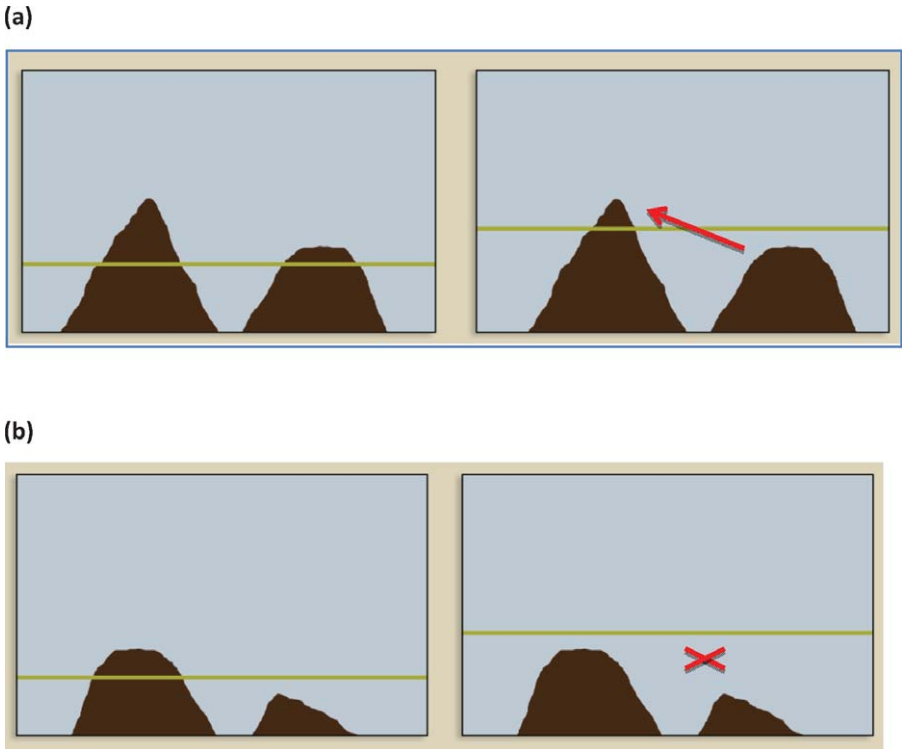

FIGURE 5. (a) Way-out scenario after the onset of an interglacial period affecting an oceanic island above-timberline summit ecosystem distribution. (b) No-way-out scenario after the onset of an interglacial period affecting an oceanic island above-timberline summit ecosystem distribution.

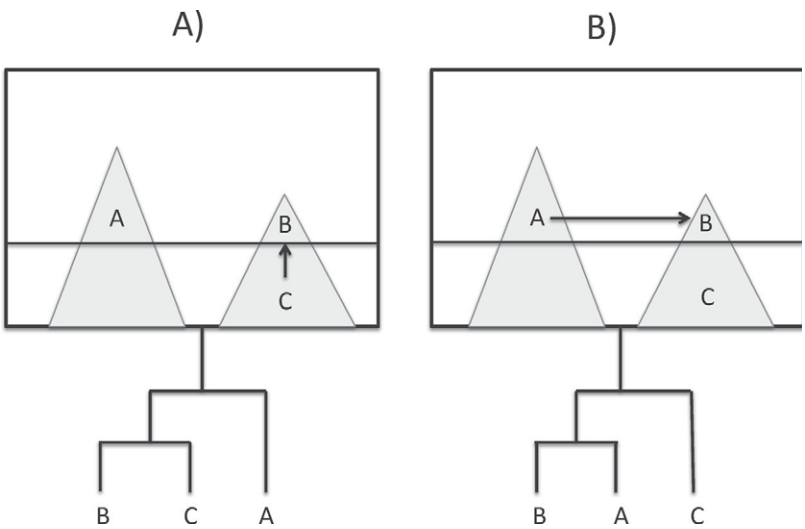

FIGURE 6. (a) Expected phylogenetic relationship for an adaptive radiation origin of a summit speciation event. (b) Expected phylogenetic relationship for a geographic speciation (vicariant) origin of a summit speciation event.

mit colonization followed by an adaptive shift (adaptive radiation) (Fig. 6, part a), whereas a closer phylogenetic relation with a species of a different island occupying the same habitat (summit) implies an interisland colonization followed by anagenetic evolution and speciation (geographic speciation) (Fig. 6, part b). Obviously, local summit extinctions or extirpations, either due to the characteristics of this very peculiar ecosystem, or due to human activities related to grazing or fire in recent millennia, may significantly confound this straightforward phylogeographic pattern.

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