

# A Multidisciplinary Approach to the Analysis of Multifactorial Land Mammal Colonization of Islands

PAUL P. A. MAZZA, SANDRO LOVARI, FEDERICO MASINI, MARCO MASSETI, AND MARCO RUSTIONI

*A highly debated question that engages paleontologists, zoogeographers, and zoologists is how terrestrial mammals colonize islands. The question's oversimplification and the subjective and partial responses to it have led to reductionist models. Insular faunas and fossil assemblages result from a complex interaction of geological, biological (in a broad sense), climatic, eustatic, taphonomic, and historical processes. Insular assemblages and their accompanying variables should be investigated on a case-by-case basis. In this article, we discuss not only common misconceptions and their potential origins but also the key issues that should be addressed when dealing with the colonization of islands by land mammals. We call for the implementation of multi- and interdisciplinary research programs and teamwork, involving paleontological, geological, and stratigraphic information; climatological factors; sea-level evolution; sampling and analytical biases; ecological, physiological, taphonomic, and environmental factors; behavioral characters and ecological preferences; genetics; phylogeography; densities of colonizing populations; and historical reports of human-mediated faunal introductions.*

*Keywords: dispersal, insular immigration, therians, modeling, vicariance*

**G**eology, climate, size, the degree of isolation, the distance from the mainland, vegetation cover, and local fauna all add to the complexity of island environments. Islands are natural laboratories for observing how ecological and evolutionary processes shape isolated communities. Islands and their communities gradually change over long periods of time; at any given point, they are the result of intricate, interdependent combinations of geological, climatological, and biological factors. It would follow that their study is an ideal case for collaboration among different kinds of specialists. Hypotheses and models developed jointly by biologists, zoologists, ecoethologists, geneticists, and paleontologists could benefit from this collaboration. Unfortunately, however, this sort of cooperation rarely occurs.

There are many examples of open or unresolved issues in the field. For example, controversy among biogeographers (Grande 1990) revolves around whether insular faunas derive from dispersal or from *vicariance* (i.e., the geographical separation and isolation of a subpopulation), but these two processes can be part of the same chronological event (Masini et al. 2002). Under the effects of sea-level changes or tectonic movements, a land bridge that originally functioned as a freely accessible, two-way connection may gradually morph into an ever-more-filtering corridor and may eventually sink, leaving an island—and its fauna—in

complete isolation. The understanding of such a complex process can be reached only by taking a multidisciplinary perspective that encompasses not only biogeographic factors but also geological processes, climatic influences, and sea-level changes.

In numerous studies, starting with Darwin's (1859) and Wallace's (1869) historical treatises and continuing into the twentieth century (e.g., Simpson 1940, McKenna 1973), contrasting modes of island colonization have been suggested (table 1). Some of the more recent researchers (e.g., Dermitzakis and Sondaar 1978, van den Hoek Ostende et al. 2009, variously inspired by Matthew 1939) have considered *sweepstake migration*—the sporadic, accidental, and highly selective dispersal from a continent to an island by way of swimming or natural rafting—as the most likely and most common process of colonization. According to some scientists (e.g., van den Hoek Ostende et al. 2009), a two-way connection with the mainland would produce balanced insular fauna or fossil assemblages (a *balanced* fauna is in a state of equilibrium). *Sweepstake colonization* (in which not all the ecological niches that occur on the mainland are actually occupied) would instead result in unbalanced insular mammal fauna or fossil assemblages. In the use of these concepts, it is assumed that the composition of either living or fossil insular mammalian communities reveals their mechanisms

**Table 1. Ways of dispersal and expected characters of insular faunas.**

| Ways of species dispersal   | Characteristics of the resulting fauna   |
|---|--|
| Corridors (pathways devoid of any physical or ecological barrier)   | Balanced (i.e., the community is sufficiently varied to be ecologically stable) nonendemic fauna |
| Filter bridges (routes open only for some species)  | Balanced faunas but impoverished in species  |
| Pendel routes (narrow sea straits that can be easily crossed by good swimmers)                              | Unbalanced faunas, with both endemic and mainland taxa   |
| Sweepstake routes (routes of sporadic, accidental, and highly selective dispersal from continent to island) | Very endemic and unbalanced faunas   |

of dispersal to islands (see Palombo 2009a and the references therein).

We contend that this is an oversimplification. Insular terrestrial mammal communities, either living or fossil, can be found to be unbalanced for many more reasons than a sweepstake invasion by new species. For example, faunal *relaxation* (i.e., the loss of species from newly isolated islands under environmental or other pressures resulting from the island environment itself, as in Brown JH 1971) and *selective preservation* (in which species exhibit different preservation potential, depending on the durability of their skeletons) need to be considered in unbalanced assemblages: Ecological, taphonomic, and stratigraphic issues therefore need to be taken into account simultaneously. Just why insular mammal communities are unbalanced is a key issue for debate in the field, as we shall see.

Increasingly, multiproxy and interdisciplinary investigations are a feature of scientific research. Here, we emphasize that solid inferences in the field of insular mammal colonization can be achieved only through cross-referencing different but mutually supportive records. We maintain that research programs in this field need to include the examination of paleontological evidence, together with geological and stratigraphic information; climate and sea-level evidence; taphonomic sampling; ecology; the behavioral, genetic, and physiological characteristics of the colonizing populations; phylogeography; species densities; and historical records of human-mediated faunal introductions. Not one of these areas, in principle, stands above the others in the search for scientific truth or models.

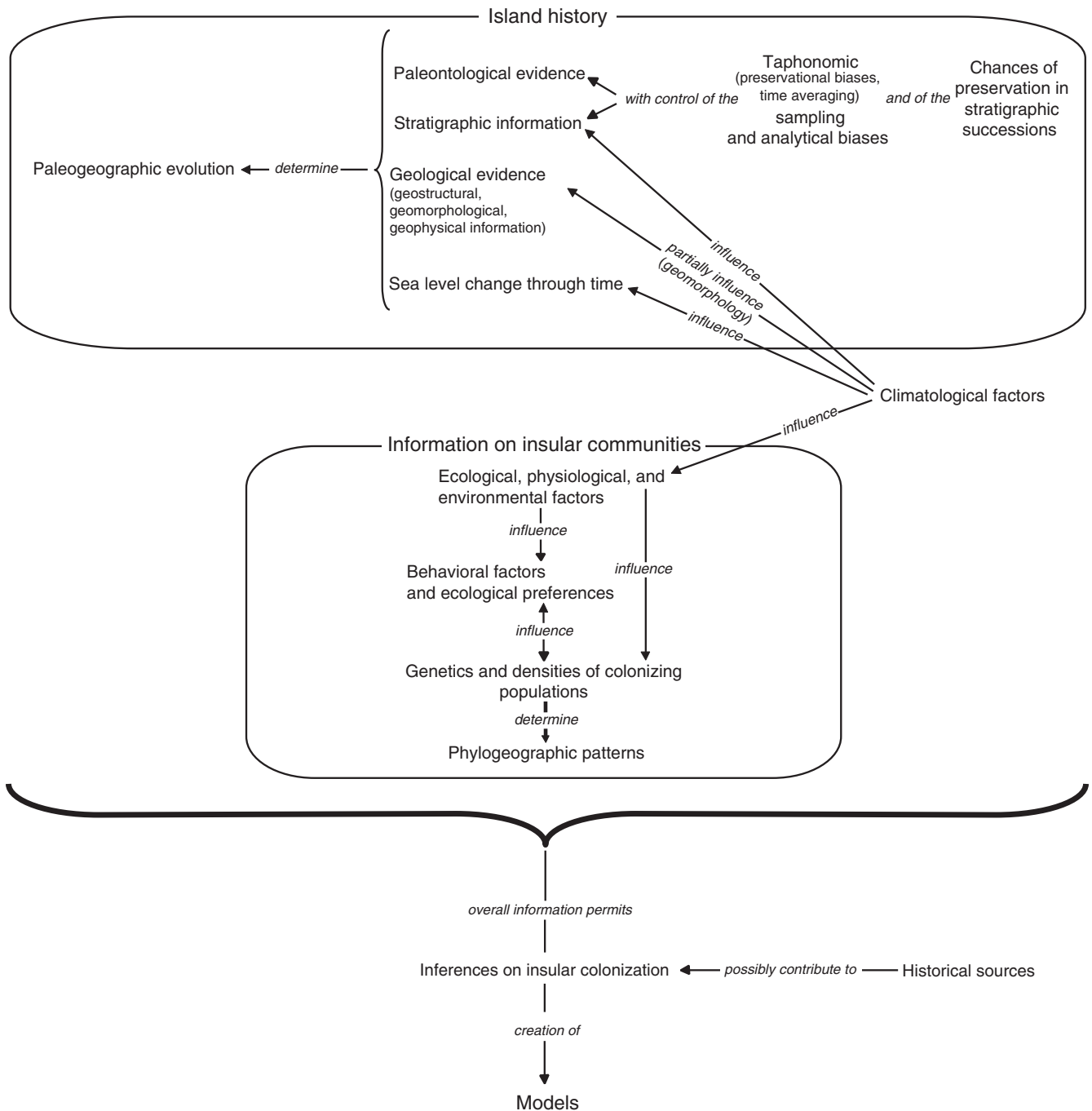
Figure 1 is a flow diagram that illustrates this principle through the key areas of information that need to be considered in the study of insular land mammals. The graph also shows the interrelations among and across the different groups of variables and the many lines of evidence.

### Geological, paleontological, and stratigraphic evidence

Many islands (e.g., the Aegean archipelago, the Indonesian islands) are located in active tectonic belts and are possibly

subject to intense deformation. Consequently, accurately interpreting geological data (the most comprehensive available and developed at the finest resolution level) is crucial in establishing the relative likelihood of various colonization hypotheses, especially because many of these hypotheses conform to a biogeographic methodology, which is dependent on geology. The fossil record, however, is the primary evidence of faunal dispersal to islands; it indicates how and from where islands were colonized and the periods during which they were isolated or connected. Because isolated faunas grow progressively more endemic as the time of isolation increases, fossils can indicate the existence of a *fossil island*—a past colony of mammals on a once-isolated landmass; they can provide details of the island's changes over time. Paleontological data can furnish useful evidence to help geologists in the reconstruction of the dynamics of landmasses and of changes in sea level. An interdisciplinary approach benefits all sides in this research: Theories can be tested against reconstructions obtained using the information of other disciplines. For example, the fossil record provides useful corroboration for geologists in their reconstructions of the dynamics of landmasses and of sea-level variation. It also helps paleoclimatologists in their understanding of how climatic conditions have changed over time. Conversely, geological and climatic events help paleontologists deconstruct colonization processes. In addition, neontologists may use the paleontological record in a comparative way to reconstruct and understand the colonization histories of modern insular communities.

Geological and paleontological events are registered in the terrestrial and marine stratigraphic successions of an island (figure 1). The accurate assessment of stratigraphic and depositional resolutions or the composition of layered successions is essential not only to estimate the age of colonization events but also to evaluate the strength of geological and paleontological information. Because of the predominantly destructive (erosional) conditions on land, terrestrial stratigraphic successions are usually highly disrupted temporal records from insignificant spatial areas (McKinney et al. 1996, Kidwell and Holland 2002). The resolution of stratigraphic sequences may, however, yield key information on the sequence and nature of geological events, as well as on the relative abundance of different components or species within a fossil community. Discontinuous stratigraphic records—or even exceedingly long stratigraphic records—may register significant short-term events, whereas long records can have the effect of averaging out many short-term variations. Some species—those with less uniform distribution in the fossil record—may appear to be more rare than those that are more evenly distributed (McKinney et al. 1996). Other difficulties can arise from a fossil-bearing stratum with reworked (exotic) particles and fossils or when sedimentary structures and diagenetic overprints (post-burial modifications) postdate its deposition, thus making its analysis more difficult. These factors can all strongly bias the paleontological and paleoecological inferences on past



**Figure 1. Data involved in the analysis of insular terrestrial mammalian communities and of their insular colonizations. The diagram shows the influence and control exercised by specific factors on the different records and the interconnections and data flows between the different fields of research. Theoretical models of insular colonization should be based on inferences drawn from two sets of data: (1) the evidence needed to reconstruct an island’s history and (2) information on past or present insular terrestrial mammal communities.**

insular life, as well as our reconstructions of past paleogeographical events and structures.

Marine stratigraphic successions, however, tend to be much more complete and continuous than terrestrial ones are. They can only be accessed if they have been exposed by tectonic disruptions and uplifts or by sea-level drops or

by directly drilling into the sea bottom. Raup (1976) also showed that the probability of preservation per unit of geological time is strongly connected with the volume of local rocky outcrop: Our detailed knowledge of any fossil record correlates strongly with the amount of rock available for sampling for the period. The marine sedimentary

deposits around islands are treasure chests of information. They can reveal possible moments of surfacing of the seafloor and, therefore, possible past land-bridge connections. Exploring them, however, requires expensive offshore coring. Consequently, many tentative theories on the land mammal colonization of islands shall remain mere working hypotheses until that information is revealed. The literature offers emblematic examples. Crete and Madagascar are often considered to have been isolated for millions of years. In fact, they harbor unbalanced endemic fossil assemblages, which would support both long isolation and sweepstake immigrations (de Vos et al. 2007, Ali and Huber 2010, van der Geer et al. 2010). The careful examination of the seafloor around islands such as Cyprus and Madagascar, for example, shows the presence of structural highs (reliefs) blanketed by as-yet-unexplored Quaternary sedimentary successions (e.g., see the Deep Sea Drilling Project, [www.deepseadrilling.org/25/dsdp\\_toc.htm](http://www.deepseadrilling.org/25/dsdp_toc.htm), which systematically bypassed the Pleistocene deposits overlying the Davie Ridge, which crosses the Mozambique Channel). From the literature, we learn, for instance, that the Plio-Pleistocene terms of the stratigraphic sequences over the northeastern underwater extension of the Kyrenia Mountains, at Cyprus, are missing or largely condensed (Aksu et al. 2005), which happens when a previously submerged structure surfaces. The same literature indicates that those structures were also affected by active Quaternary tectonics and volcanism. The Quaternary is a time during which the sea level fluctuated, sometimes dropping 120–130 meters, in response to a cyclic climatic forcing. We can speculate that the interplay of tectonics and sea-level low stands may have temporarily created connections with the nearest mainland, at least during the most severe glacial periods, which would have favored the colonization of those islands.

Biogeographic studies of the Galápagos Archipelago also show how biogeographic models are often geologically dependent. Geological consensus favors the *oceanic* origin of the archipelago—that is, entirely volcanic and with a seafloor composed of oceanic plates (cf. Bowman et al. 1983). This geological model allows only for overwater dispersal or for so called *stepping-stone* colonization. Grehan (2001) reviewed an alternative model, developed by Croizat (1958) and corroborated by the plate tectonic solution proposed by Holden and Deitz (1972): the Galápagos Gore. In this scenario, the Galápagos biota would have been inherited from a whole series of ancestral Galápagos Islands located on the eastern Pacific plate, which is called Cordillera and which progressively merged with North, South, and Central America between the Mesozoic and the Cenozoic Eras.

### Taphonomic sampling and analytical biases

Returning to the issue of unbalanced assemblages, not all species fossilize with the same degree of detail or frequency. The stratigraphic record of paleontological events is highly dependent on taphonomic—fossilization—processes (figure 1), and taphonomic biases exist against rare species

and species with a low potential of preservation (Lyman 1994). An insular fossil assemblage might in truth be unbalanced because of preservational biases rather than sweepstake colonization, or through a combination of these factors. Moreover, rare species have a low chance of being included in the fossil record (McKinney et al. 1996).

Carnivores are a case in point. The reason for which large carnivores are apparently absent from insular fossil records could be related to various factors. Carnivores are usually rare in insular faunal communities; however, in areas in which food abundance and space are limited and competition is the most fierce, as on islands, they are essentially even rarer. In the fossil record, they virtually disappear. The chances that carnivore bones, which are so statistically sporadic, can survive all potential *post mortem* destruction and that a (rare) stratigraphic sequence can capture evidence of them are, in fact, very low. Only the *biostratinomic* (i.e., *post mortem* and preburial) accumulation and concentration of carcasses and bones under certain conditions, such as in natural *conservation traps* (e.g., caves or natural pits), increase the probability of carnivore fossilization (Masseti 1995). In general, *post mortem* transport of the remains of a taxon by biotic (e.g., carnivores, scavengers) or abiotic agents (e.g., stream) to areas extraneous to its original habitat is negligible (Kidwell and Holland 2002).

Temporal resolution and the usually heterogeneous patterns of many fossil records contribute to the variability of single stratigraphic successions and to the balanced or unbalanced nature of a fossil assemblage. However, the voids of information within each stratigraphic section can be filled by combining paleontological data from multiple sections and sedimentary basins (Kidwell and Holland 2002). This would strengthen any colonization hypotheses. But islands, being *de facto* a limited physical space, often prevent such composition of paleontological data because of the rarity of fossiliferous stratigraphic sequences, which adds to the difficulty of reaching any firm conclusions.

Taphonomic analysis is further confounded by *time averaging*, whereby animal remains may build up over time through attrition, forming accumulations that mimic natural communities. Kidwell and Behrensmeyer (1993) showed that the time span represented in any fossil assemblage may vary over many orders of magnitude. The more a fossil assemblage is attritional, the higher the probability is that it is an artificial combination of communities from distinct climatic or sea-level change events scattered over time. In order to reconstruct the ecological characters of insular communities, the different colonizers must be treated as having equal preservational potential, which is seldom—if ever—the case, as was mentioned above. There follows a strong desire in analyses of such insular communities to disentangle these data and to establish their true ecological characteristics—that is, the faunal interrelationships and the degree of balance or unbalance and of diversity at any one point in time. Despite the flurry of studies on insular endemic modifications, little attention has been paid to

methodological limitations and inaccuracies. Little research has been devoted to the impact that insufficient sampling and inadequate sampling techniques, together with imperfect taxonomic determinations and improper data recording during recovery, have had on the study of insular colonization. How much do these biases weigh on the diagnosis of an “unbalanced” fossil assemblage?

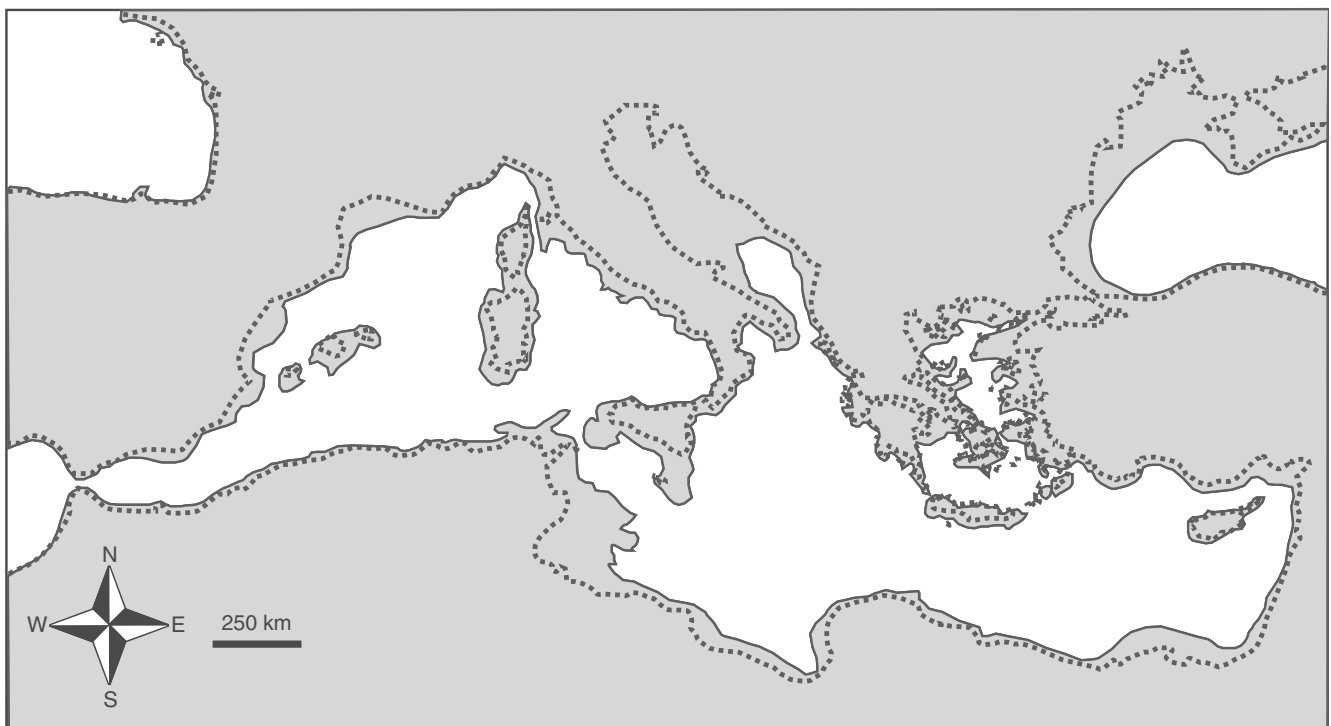
### Climatological factors and eustatic evolution

Climate has a profound influence on the diversity patterns of insular mammals. Because mammal communities cannot quickly move off of islands, they are heavily affected by climatic variation. Insular communities can withstand only limited and slow changes, and species turnover is significantly higher than in continental mainland contexts (Lomolino et al. 2010). Climate-driven selection can easily lead to unbalanced insular land mammalian communities. The contribution of paleoclimatology can also explain the tempo and mode of the evolution of insular ecosystems in general and of insular land mammal communities in particular (see figure 1).

The Quaternary was a time of frequent and intense climatic change. During the Pliocene Epoch, the average temperature and humidity steadily dropped, because of alternating climatic conditions (see Sarnthein et al. 2009 and the

references therein). Environmental instability affected biotic ecosystems. Climate-induced *ecological release* (the expansion of habitat and resource use by certain species in areas with lower diversity) can have serious consequences within the restricted and sensitive settings of islands. An insular ecosystem can be variously restructured and renewed in direct and relatively rapid response to climate change impacts.

Sea-level oscillations can create or destroy physical and ecological connections and barriers, which can promote habitat uniformity or fragmentation (see figure 2). In the course of the Quaternary, extensive, climate-driven sea-level variations had severe consequences for landform-shaping processes. How the global sea level has changed over time is now fairly well known (cf. Miller et al. 2005), but the reconstruction of sea-level fluctuations at more local levels is still in the early research stages. Knowing how paleogeographic settings varied in response to eustatic changes (figure 1) is crucial to understanding how and why mammal communities of continental islands started and continued or disappeared over time. The often-clear correlation between well-dated insular fossil communities and sea-level variations could, in fact, be indicative of a causal relationship, with eustatic events driving biological ones (e.g., Madagascar; Warren et al. 2010). Coming to



**Figure 2.** The Mediterranean during the peak of the Last Glacial Maximum (approximately 18,000 years ago). The example shows how common island connections to the mainland are during sea-level low stands. The dotted contour represents the present-day Mediterranean coastline. Global, climate-driven sea-level variations and geological dynamics can either open or close the way to islands. This regulates the influx of land mammals on islands, with chain reactions determining ecological settings, behavioral and physiological responses, population density patterns, and gene flow. Abbreviation: km, kilometers. Source: Adapted with permission from Thiede (1978).

firm conclusions about land mammal insular communities, however, is often prevented by the stratigraphic uncertainties of the fossil record in most island contexts. In many instances, this kind of eustatic–fossil correlation would be the deciding factor between alternative hypotheses of insular colonization.

The Quaternary Period includes 103 climatically driven sea-level variations (Miller et al. 2005), some of which greatly exceed 100 meters in magnitude. However, just how often or to what extent have researchers cross-correlated geological evidence from islands with these sea-level variations when trying to establish periods of connection with mainland areas? And just how much has this geological and eustatic history been compared with the paleontological evidence available?

### Ecological and physiological factors

The physiology, ecological dynamics, and environmental choices of land mammals in insular settings are the areas most investigated by (paleo)biogeographers and paleontologists in their search to understand dynamic evolutionary processes on islands, but they are also the topics that have provoked the most heated debate. The results of decades of insular-ecosystem research clearly show that various ecological causes account for the unbalanced character of many living insular mammalian communities (Palombo 2009b). Paleontologists could benefit from this invaluable information by concluding that unbalanced fossil insular mammalian communities are not necessarily the indisputable result of sweepstake colonization.

**Island colonization, an ecologically selective phenomenon.** Ecologists can help to show that island colonization and the composition of insular communities or assemblages are governed by a high level of natural selection and species extinction. Different levels of susceptibility to extinction, abilities to migrate, and other vulnerabilities or capabilities can lead to different responses in and among species in insular settings (Lawlor 1986). *Relaxed* community fossil assemblages (Brown JH 1971) are those in which a species' richness decreased over time, as, for example, when the more resource-demanding taxa (e.g., large specialist carnivores) became extinct, which would have allowed smaller-sized generalists to develop higher population densities. Different levels of vagility, vulnerability, and susceptibility to extinction can lead to different responses among species in insular settings (e.g., Lawlor 1986). An example is offered by the rapid disappearance of over 75% of the original vertebrate species from the small- and medium-size islands that were created by the flooding of the mountainous areas of Panama when the Panama Canal was opened (Terborgh 1974).

Some paleontologists relate the selection of species that can be found on islands to those species' swimming skills and have argued that the presence or absence of specific ungulates in insular fossil assemblages is a result thereof (see de Vos et al. 2007 and the references therein, van den Hoek

Ostende et al. 2009). Taxa not normally found on islands either today or in the past, such as perissodactyls, are deemed to be poor or short-distance swimmers (de Vos et al. 2007). In contrast, cervids (e.g., giant deer or red deer), which are frequently found in insular fossil communities, are considered to be good and long-distance swimmers. In spite of the fact that ecoethologists can give valuable information about the swimming abilities of the living counterparts of past land mammals (see below), the presence or absence of land mammals on islands may very well depend on the vagaries of climate change, as well as on the island's resources, size, degree of isolation, and microclimatic conditions. However, perhaps most important is the vegetation at the supposed time of colonization and thereafter. Opportunistic feeders, including red deer and goats (e.g., *Myotragus*), are selectively favored as island colonists over concentrate selectors, such as large bovids, and grass and roughage eaters, such as equids (e.g., Hofmann 1989). This may explain why Megaceroid deer, red deer, and goats are (or were) so successful on islands, whereas roe deer, horses, and large bovids are (or were) so rare or thoroughly absent.

Equids may also be absent from islands for other reasons. Wetlands and thick, humid tropical rainforests, such as those of southeast Asian archipelagos, act as ecologic filters, keeping out equids but admitting certain kinds of rhinoceroses. In fact, forest-dwelling rhinoceroses established on Luzon (Philippines), possibly from Indochina, and on the Japanese islands. During Late Pleistocene sea low stands, these islands were connected repeatedly with the mainland and could easily be reached by roaming rhinoceroses. Convoluted explanations of island colonization based on animal buoyancy or swimming skills enhanced by intestinal gasses (de Vos et al. 2007) could easily be avoided by closer collaboration among paleontologists, geologists, paleoclimatologists, and ecologists, as we have said before.

Another erroneous attribution of causality, again through a lack of cross-disciplinary reference, is the widely held belief—due to the absence of large carnivores—that many fossil insular assemblages are highly unbalanced (e.g., de Vos et al. 2007, van den Hoek Ostende et al. 2009), despite the hard evidence that the number of different species of insular carnivores—large ones included—is considerable (table 2). Islands with wetlands and intricate, humid tropical rainforests are indeed unsuitable for social carnivores, such as canids and lions, who need vast expanses of physical territory in order to ensure the survival of a minimum population size. Nonetheless, forests are the ideal habitat for solitary ambush predators, such as jaguars, leopards, and tigers; although leopards and tigers do reach islands covered with forests (table 2), felids seem to have never undergone endemic modifications on islands. In fact, the differences between insular felids and their mainland ancestors never range beyond the subspecific level—for example, the Japanese Iriomote cat (*Prionailurus bengalensis iriomotensis*) and Tsushima cat (*Prionailurus bengalensis euphilura*) are still genetically close to the continental leopard cat (*Prionailurus bengalensis*;

**Table 2. Insular carnivores.**

| Location                        | Species   |
|---------------------------------|---|
| Arctic islands                  | <i>Ursus maritimus</i> <sup>b</sup> , <i>Vulpes lagopus</i> <sup>c</sup>  |
| Mediterranean islands           | <i>Chasmaportetes mele</i> <sup>b</sup> , <i>Cynotherium sardous</i> <sup>c</sup> , <i>Crocota crocuta</i> <sup>b</sup> , <i>Canis lupus</i> <sup>c</sup> , <i>Ursus arctos</i> <sup>b</sup> , <i>Panthera leo</i> <sup>b</sup> , <i>Canis aureus</i> <sup>c</sup> , <i>Vulpes vulpes</i> <sup>c</sup> , <i>Martes martes</i> <sup>c</sup> , <i>Martes foina</i> <sup>c</sup> , <i>Meles meles</i> <sup>c</sup> , <i>Mustela nivalis</i> <sup>c</sup> , <i>Lutra lutra</i> <sup>c</sup> , <i>Enhydriactis galictoides</i> <sup>c</sup> , <i>Genetta plesictoides</i> <sup>b,c</sup> |
| Madagascar <sup>a</sup>         | <i>Fossa fossana</i> <sup>c</sup> , <i>Eupleres goudotii</i> <sup>c</sup> , <i>Gallidia elegans</i> <sup>c</sup> , <i>Galidictis fasciata</i> <sup>c</sup> , <i>Mungotictis lineatus</i> <sup>c</sup> , <i>Salanoia concolor</i> <sup>c</sup> , <i>Cryptoprocta ferox</i> <sup>c</sup>  |
| Zanzibar                        | <i>Panthera pardus adersi</i> <sup>b</sup>  |
| Southeast Asian islands         | <i>Prionailurus viverrinus</i> <sup>b</sup> , <i>Prionailurus bengalensis</i> <sup>b</sup> , <i>Neofelis nebulosa</i> <sup>b</sup> , <i>Paradoxurinae</i> <sup>b,c</sup> , <i>Hemigalinae</i> <sup>b,c</sup> , <i>Panthera pardus</i> <sup>b</sup> , <i>Panthera tigris</i> <sup>b</sup>  |
| Japanese islands                | <i>Prionailurus bengalensis iriomotensis</i> <sup>b</sup> , <i>Prionailurus bengalensis euptilura</i> <sup>b</sup>  |
| Falkland islands                | <i>Lycalopex griseus</i> <sup>c</sup>   |
| Channel islands, off California | <i>Urocyon littoralis</i> <sup>c</sup>  |

<sup>a</sup>All from a single colonization event. <sup>b</sup>Hypercarnivore.  
<sup>c</sup>Mesocarnivore.

Masuda and Yoshida 1995). Once again, neontological data can show that more resource-demanding hypercarnivores (i.e., those with more than 70% of their diet consisting of meat) are more vulnerable on islands than are meso- (meat between 50% and 70% of their diet) and hypocarnivores (meat less than 50% of their diet) and that they rapidly disappear (O'Regan et al. 2002).

**Faunal interaction.** Species interaction is yet another fruitful area for research into past insular land mammals. Studies of insular ecology have been focused particularly on competition (e.g., Raia and Meiri 2006), as opposed to parasitism, predation, or mutualism. However, the former is not always the deciding factor in the ecology of larger, more heterogeneous islands: Research shows that these islands tend to carry more-diverse biotas than do smaller islands with ecologically similar species peacefully occupying distinct and separate areas, as in a checkerboard configuration (Diamond 1975). Large islands can offer essential space to pioneer species that then create new niches for other potential immigrants (Lomolino et al. 2010). However, competition could be the reason that ecologically similar species do not often coexist on smaller islands. Species interaction can limit biodiversity and may result in impoverished and probably also unbalanced communities but can also create new chances for evolution for certain species. In addition, habitat fragmentation, whether within larger islands or between islands, greatly affects immigration and extinction patterns, increasing or reducing colonization success. Ecological studies are therefore another valuable resource in the interpretation of insular fossil records.

**Natural rafting, a still unexplored solution.** Overseas dispersal by natural rafting is often advocated to explain *biogeographic conundrums*—that is, the baffling presence of vertebrates, invertebrates, and some plants, especially of salt-intolerant taxa, on oceanic or oceanic-like islands (cf. Ali and Huber 2010). The idea is that violent storms might have dislodged large masses of vegetation that were then carried down rivers and out to sea, forming temporary islands on which animals could take refuge. Dispersal then required favorable currents by which species rapidly traversed stretches of saltwater. This kind of sweepstake dispersal theory is currently enjoying vast popularity and has been readily embraced—perhaps too enthusiastically—by both neontologists and paleontologists. In fact, doubts are starting to emerge (Stankiewicz et al. 2006, Masters et al. 2007). How much attention is paid to the actual physical and physiological characteristics and capacities of land mammals? Crossing oceanic stretches would expose them to large temperature and humidity variations, to high concentrations of salt, and—more problematic for land mammals—to a prolonged lack of food and water. We can suppose that they traveled in torpor or in states of hibernation and, therefore, at metabolic levels lower than normal (Ali and Huber 2010). However, not all mammals are capable of lowering their metabolic levels to any significant degree, nor of spontaneously arising from metabolic torpor when conditions change. Terrestrial mammals, especially larger ones, are at a disadvantage relative to other animals because of their high energy requirements. In contrast, they are more effective thermoregulators than *poikilotherm* animals (i.e., those with variable body temperature) and smaller mammals and can therefore cope with temperature instability more effectively (Masters et al. 2007). Moreover, terrestrial mammals rafting across sea straits would need to do so in sufficient numbers to successfully colonize an island over time. Small colonizing populations are more sensitive to genetic drift and show increased inbreeding and relatively low genetic variability. There is a critical number of individuals required to avoid extinction or the unsteadiness of genetic drift (Reed et al. 2003).

Accounts of land mammals observed on floating mats of vegetation are rare and, in most cases, anecdotal. Monkeys and rodents have been seen on floating debris in rivers (van Duzer 2004), where drinkable water is readily accessible, unlike under sea conditions. How long would those animals survive in transoceanic dispersal? Prescott (1959) reported the case of a jackrabbit (*Lepus californicus*) found perched on a pelagic raft of giant kelp (*Macrocystis pyrifera*) some 24 kilometers (km) southeast of one of the three Channel Islands off the coast of San Clemente, California. The animal was in a very poor condition. This is the only account available in the literature in which a terrestrial mammal was observed to be traveling on flotsam across a stretch of seawater. Moreover, this example actually speaks against island colonization through natural rafting in that no jackrabbits are reported to inhabit any of the Channel Islands, despite the fact that *L. californicus* has been present

in western North America since the early Irvingtonian Age, over 1.5 million years ago (Barnosky 2004). In all this time, rafting jackrabbits have never colonized any one of the three Channel Islands, which are located, at most, 120 km off the California coast.

Natural rafting raises many more problems than it solves. Accurate integrated ecoethological and physiological tests; population genetics studies; and geological, paleogeographic, and paleoceanographic reconstructions are required before rafting can be proposed as a plausible hypothesis for the colonization of islands at any distance.

### Behavioral factors: Swimming to colonize

Climatic changes and ecological contexts need to be carefully defined before any conclusions are reached about their impact on animal behavior; in fact, these changes can be environmentally dependent (figure 1) and can be mediated by epigenetic mechanisms (Ledón-Rettig et al. 2013). Rapid epigenetic behavioral variation facilitates population survival wherever environmental change is too rapid for genetic modification to arise. This is therefore an important adaptive resource under unstable and rapidly changing environmental conditions, such as on islands.

Such models of animal behavior form the basis of many hypotheses of island colonization through overwater dispersal. However, the swimming skills and propensity to venture into water of many land mammals are sometimes overrated or inaccurately represented. Although substantial bodies of water can occasionally be accidentally crossed by one-way sweepstake dispersers, as in the case of natural rafting, they normally act as filtering passages—technically, *pendel routes*, which can be crossed in both directions only by good swimmers (Dermitzakis and Sondaar 1978) or by animals predisposed to venture into water. Swimming is neither easy nor natural for most terrestrial mammals, although most can swim after a fashion. It would follow that any swimming or behavioral hypotheses would significantly benefit from a minimal cross-checking with ecoethologists.

Cervids and elephants are capable swimmers, however. Thanks to their streamlined body shape, cervids are potentially more agile swimmers than elephants are (Held 1989). However, empirical observations reveal that deer do not swim very often (Vigne and Marinval-Vigne 1988) and cannot swim long distances—only managing a consecutive 2–3 km swim, on average (Brown D 2005)—and need to have the opposite shore within sight (Severinghaus and Cheatum 1956). Cervids whose swimming performance has been reported in the literature are always at least as large as fallow deer.

Elephants, however, seem to be able to swim almost 50 km (Johnson 1980), owing to their unique lung anatomy, while using their trunks for snorkeling (West 2001). Because they tend to swim in herds, elephants can reach islands in relatively high numbers and can therefore form sufficiently varied gene pools, which increases the chances of successful colonization (see below).

Suids seem to be proficient swimmers (Oliver et al. 1993). Whether hippopotamuses can swim or even float is another issue of contention. Many researchers (Marra 2005, Ali and Huber 2010) consider them excellent divers and swimmers in view of their aquatic lifestyle. However, according to earlier studies (e.g., Eltringham 1999, Fisher et al. 2007) and more recent studies (Coughlin and Fish 2009), hippopotamuses do not swim at all. The structure of a hippopotamus's body seems to be designed to overcome buoyancy, which helps it keep its feet firmly stuck to the water bottom while also preventing its barrel-shaped body from rolling, thus avoiding unstable motion (see Coughlin and Fish 2009 and the references therein).

Another factor mitigating against any kind of oceanic crossing by hippopotamuses is that they naturally avoid deep water. Under normal circumstances, juveniles resurface to breathe every 2–3 minutes and adults every 3–5 minutes (Eltringham 1999). They also do this automatically when sleeping underwater (Jackson and Gartlan 1965). The hydrostatic pressure in deep water would prevent this behavior.

Supposing that hippopotamuses cannot swim, a possible alternative to explain their presence on islands is that of passive transportation by rafting, but this hypothesis is highly implausible, for a number of reasons. Adult hippopotamuses weigh from 1.5 to 3 metric tons: How thick does a tangled mat of vegetation need to be to act as a seaworthy raft to carry several individuals of this size? Moreover, hippopotamuses need to drink large amounts of water daily (Calder 1984) and are very sensitive to exposure to solar radiation.

Hippopotamuses reached land-bridge islands, such as the British Isles, Sicily, Malta, and Mafia. In the course of the Quaternary, temporary connections between land-bridge islands and their nearest mainland areas were recurrently created by the favorable interplay of regional uplifts, glacioisostatic rebounds, and high-amplitude glacio-eustatic changes. But hippopotamuses also colonized Crete, Cyprus, and Madagascar, which are classified as oceanic or oceanic-like islands (e.g., van der Geer et al. 2010). If hippopotamuses cannot swim, oceanic island colonizations are difficult to explain. In the absence of a credible alternative explanation, the presence of hippopotamuses on islands suggests the existence of (perhaps filtering but walkable) land-bridge connections. Here, we can see how the adoption of a multi- and interdisciplinary approach is essential to understanding events in their full complexity.

Large terrestrial carnivores are absent from unbalanced insular faunas. For this reason, some scholars consider those species poor swimmers (de Vos et al. 2007, van den Hoek Ostende et al. 2009). The numerous sightings and fossil records of carnivores on islands would seem to contradict this opinion (table 2). Leopards and tigers have been repeatedly sighted in southeastern Asian islands, as was mentioned above.

As has already been discussed, the lack of large carnivores from insular faunal or fossil records can be explained by



ecological incompatibilities, as was predicted by the relaxation theory, or by preservational biases, as in the case of fossil assemblages, in which some kinds of animal remains have low probabilities of being preserved by rare insular stratigraphic successions (O'Regan et al. 2002). In these cases, swimming abilities or their absence in these animals are not part of the bigger picture.

Small mammals are often good but short-distance swimmers. Empirical observations indicate that rodents normally swim, at most, only few hundred meters, with the exception of Norway rats and red squirrels, which can swim up to 2 km (Russell and Clout 2005, Fritts 2007). Rodents cannot reasonably be expected have crossed the 972 km of ocean range separating the Galápagos Archipelago from Ecuador's shoreline (van den Hoek Ostende et al. 2009). It seems therefore unrealistic to posit that short-distance-swimming micromammals colonized the Galápagos Islands through stepping-stone immigration and even less so through natural rafting. Furthermore, the difficulties of reaching any firm conclusions about the colonization of the Galápagos Islands are compounded by the commonly held assumption that they are of oceanic origin, as was explained above. This is another example in which coordinated multi- and interdisciplinary research among scientists could be a reciprocally rewarding approach.

But what drives terrestrial animals into an alien environment such as water? Density-dependent factors, such as competition, the search for food and partners, or—conversely—predation (see Lomolino et al. 2010 and the references therein) seem to be logical factors. However, attempts to evade capture, predators, and aggressive conspecifics or flight from floods or fires may also be relevant, but random events and sheer chance could, in many cases, be the real reasons for animals' venturing into water in search of new territories (Severinghaus and Cheatum 1956, Brown D 2005).

### Genetics and densities of colonizing populations

Unstable factors and circumstances affect the population size and density of any group of animals, and these effects are hard to quantify, especially *post hoc*, in fossil assemblages. Furthermore, in any ecological environment, the number of conspecifics, population density, and individual fitness are dynamically interrelated (i.e., the Allee effect; Stephens et al. 1999) and correlate with an environment's carrying capacity (figure 1; Barton and Turelli 2011). The subtle interplay of these parameters establishes the critical density threshold under which a population is doomed to extinction and above which it can increase deterministically (Barton and Turelli 2011). A small colonizing population is more sensitive to environmental and demographic *stochasticity* (random unsteadiness; Stephens et al. 1999). A population of land mammals might theoretically accumulate on an island through successive colonizations, but the length of time that would be required to ensure stable colonization would be far too long. The maximum number of individuals

that can live on an island is determined by the island's carrying capacity, which varies.

It follows that terrestrial mammals can become established on an island only if they arrive in sufficient numbers and if the circumstances on the island allow for a local deterministic increase in population. Quite naturally, any population of colonizers that detaches from a larger mainland population experiences a loss of genetic variation (i.e., Mayr's 1942 *founder effect*) and diverges from the mainland population both genetically and phenotypically. The colonizers also show increased inbreeding.

Excluding freely accessible, two-way corridor bridges, a key issue that needs to be addressed jointly by genetists, biogeographers, and paleontologists is whether filtering corridors and sweepstake modes of immigration allow for the passage of a sufficient critical number of individuals to ensure the survival of colonizing species. To successfully colonize an island, a swimming taxon needs not only to be a good swimmer, predisposed to venturing into water, but also to be an *r-strategist* (i.e., it must have high reproductive potential and a limited or no requirement for parental care). Deer, hippopotamuses, and elephants, which are found on many islands around the world, are *K-selected* animals (i.e., they produce fewer offspring and often practice extensive parental care; Eltringham 1999, Moore 2007). This suggests that individuals in insular settings probably undergo (perhaps genetic) changes that collectively contribute to maintaining sufficiently varied gene pools or to increasing genetic variability. Apparently, settlements on islands may be consolidated by transitions from a *K*-strategy to an *r*-strategy (in the early stages of colonization) and then back to a *K*-strategy (i.e., specialization and low birth rate; Lomolino et al. 2010).

At the initial stages of colonization, very small populations of immigrants are sensitive to environmental and demographic unsteadiness, but the endemic modifications shown by insular invaders are strikingly recurrent. Insular species' body size is constrained by multiple complex factors (Meiri 2007). *Ecological release* (i.e., the introduction of a taxon to an environment other than its original habitat) typically promotes gigantism in small vertebrates (McNab 1994). In contrast, resource limitation promotes dwarfism in large-size taxa (Anderson and Handley 2002). Therefore, these seem not to be random but, rather, channelized evolutionary processes; that is, they are strongly constrained by functional and adaptive limitations and perhaps also by morphogenetic or constructional and phylogenetic confinements. Millien and Damuth (2004) cite examples that result from geographical confinement and limited resources, in line with Van Valen's (1973) island rule (according to which large species on islands tend to become nanoid, whereas small ones become gigantic).

In analyzing the relationship between body size and distribution patterns, Marquet and Taper (1998) observed that both large- and small-size species with low density and highly variable body size are best adapted to large territories

and are at greater risk of extinction in smaller ones. However, medium-size species (of about 100 kilograms) are able to form denser populations in smaller areas and are better able to adapt to islands, in general. Therefore, smaller islands best support only medium-size animals. These considerations led Marquet and Taper (1998) to state that the average body size of a species can indicate the minimum area it needs for survival. Large terrestrial mammals rapidly evolve to lose size and reduce their energy needs on islands and, therefore, increase their chances of survival (McNab 1994). For the reason explained above, equids do not spontaneously colonize islands by crossing water straits, but some human-introduced equids have developed dwarf representatives in insular contexts. Domestic horses and donkeys became smaller after their introduction onto some Mediterranean islands (cf. Masseti 2002).

Large mammal species that evolve smaller body sizes and reduce their resource requirements can produce larger and denser populations, thereby gaining gene-pool richness and eventually lowering their risk of extinction. In contrast, by reducing reproductive output and growing in body size (Adler and Levins 1994), smaller mammals lower their mass-specific maintenance costs. Because of their comparatively higher body surface-area:volume ratio, smaller individuals necessitate a high energy intake to maintain body heat (Calder 1984). Therefore, having migrated onto islands, individuals of species that are usually of large or small size in mainland areas converge toward ideal medium sizes (Millien and Damuth 2004). A corollary to these conclusions is that, being more protected from the uncertainties of the environment by their denser populations, but also by their potentially richer and more varied gene pools, terrestrial mammals living in flocks are expected to be somewhat more successful in colonizing islands than more solitary taxa would be.

The conclusion of this reasoning is that, in order to favor the necessary adaptations to insular conditions and assure community survival, land mammals need to colonize islands with a critical and substantial number of individuals. The question is whether a sweepstake process of immigration could ever ensure those numbers.

### Phylogeography

The analysis of the spatial distribution of genotypes and of genealogical lineages needs to be based on phylogenetic analysis. The resulting *phylogenies*, or evolutionary histories, are constructed from genetically controlled features, such as morphology or behavior, and from gene-sequence analysis.

Gene-sequence analysis provides the basis for determining phylogenetic relationships and morphology: It drives many neontologist models, including the calculation of the timing of colonizations and the evolutionary and ecological interactions between colonizing and resident species. However, phylogeographical inferences with limited or no paleontological, geological, and paleoclimatological verification might lead to highly controversial conclusions

(e.g., such as those in Pulquério and Nichols 2007, which showed great discrepancies in the dates of evolutionary events obtained using the molecular clock). *Paleoecology*, which outlines the habitat requirements of colonizing species (figure 1), is a particularly important aid to phylogeographers. All of these disciplines play a key role in providing the historical framework for reliably interpreting relationships among molecular sequences.

### Historical accounts

More recent history can help supply paradigms for and help formulate the reconstruction of insular colonization events. Occasionally and unexpectedly, historical and documentary sources from museum collections or zooarcheological data can supply crucial information to understand otherwise inexplicable occurrences or biotic changes on islands. It is well known that many pests (such as mice and rats) were involuntarily introduced onto islands by human colonizers. Through Varro (*De re rustica* 3.12.1), for example, we know that releasing hares on islands was an ancient Roman practice that was maintained up to his time in the so-called *leporaria*. Animals were introduced on islands to create game parks. This was still customary during the Middle Ages, when sailing ships distributed rabbits on islands as a source of food for sailors (McNitt et al. 2000). The introduction of alien organisms onto islands by humans may have often been significantly ecologically disruptive (Courchamp et al. 2003); it is, however, relatively easy to reconstruct.

We cannot exclude the possibility that answers to some biogeographic conundrums might lie buried in neglected historical records and might be related to intentional or accidental human-mediated faunal translocations. Therefore, collaboration with historians could be another important approach in this field. The historical biogeography of insular land mammals is, in our view, one of the most promising directions for future multi- and interdisciplinary research and a key area for probable breakthroughs and collaboration.

### Conclusions

As we have seen, islands and insular faunas and fossil assemblages develop as the result of a complex range of interconnected events, conditions, and processes. Insular speciation, itself, and rates of immigration or of extinction of insular biomes, ecosystems, and communities are often greatly influenced, not just by the geological, geomorphological, and geographic evolution of islands but also by eustatic fluctuations, changing climatic and ecological conditions, and epigenetically driven behavioral changes.

Because this network of intricate interdependent variables needs to be defined and analyzed, it would seem imperative that any study of insular community characteristics or any reconstructions of the processes of insular community formation would need to encompass large-scale, evidence-based, multidisciplinary approaches.

Indispensable starting points from which to detect possible biases in the relevant data sets are often initially determined both by detailed taphonomic screening and by solid stratigraphic analysis. The confluence of paleontology and geology is essential in revealing the chronological constraints that might impinge on the duration of particular bone beds and in ascertaining the uniformity of the assemblages themselves. This cross-referencing ultimately allows for the evaluation of the reliability and strength of different data. The dating of biological events—that is, the biochronology of succession of endemic fossil assemblages—is, furthermore, very useful in a wider context, to geologists who are trying to determine the interrelations between different structural units within any geological succession. Similarly, unraveling the geological and geographic history of islands, as well as revealing and dating their possible relationships with mainland areas, is as important to paleontologists as it is to biogeographers. Learning whether a piece of land has always been isolated or whether and when that land ceased to be an island is crucial in establishing the origin and development of insular communities. It would follow that the other disciplines mentioned in this study intersect with and enhance each other in similar ways. For example, cross-checking the geological evolution of islands with sea-level variations can reveal previously undetected island–mainland connections. Climate-driven eustatic sea-level changes, in turn, influence the development and disturbances of insular ecosystems. Knowing the prevailing climatic conditions at any point in time and cross-referencing this information with the ecological preferences of the inhabitants of islands may explain species discontinuities already indicated by nonuniform assemblages. Geologists, paleontologists, taphonomists, stratigraphers, paleoclimatologists, and paleoceanographers, therefore, all potentially contribute to the building of a historical framework for the most-effective neontological research on insular mammals. However, biologists, biogeographers, ecoethologists, and geneticists provide comprehensive data sets on the behavioral and physiological features of particular species, their ecological characteristics and environmental choices and possible ecological interactions, their genetic compositions and epigenetic changes, and their phylogenetic relationships. More recent data, both historical and current, on the population dynamics of extant natural insular terrestrial mammal communities and of living counterparts of previously insular faunas or of extant equivalents of past taxa provide a solid foundation and theoretical testing ground for paleobiological reconstructions, hypotheses, and colonization models.

Researchers of islands are therefore confronted by a tangled network of related variables, which, quite naturally, points toward the study of each island, past or present, on a case-by-case basis. It would seem inevitable that conclusions of a generalizing nature would inevitably be made from such studies. Nevertheless, some caution should be exercised, in that these conclusions should be reached only after at least some or possibly many of the above-discussed

factors and aspects have been thoroughly investigated and either discounted or incorporated.

The strength, credibility, and applicability of our reconstructions of insular evolution and colonization are strongly dependent on the solidity of data sets. Ignoring such a heuristic principle may produce a split in the scientific community between those who tend to rely on models and those who believe that empirical evidence is the only “true” source of information, whereas, in fact, as with disciplinary cross-fertilization, a mixture of the two approaches is needed in all cases.

### Acknowledgments

We are greatly indebted to Marco Festa-Bianchet and Adrian Lister for their invaluable advice and assistance. A previous draft also benefited from the critical reading of Shai Meiri. We also thank Kate Eadie for the language editing. This study was financially supported by PRIN (Research Projects of National Interest) 2009 MIUR (the Italian Ministry of Education, University and Research) grants.

### References cited

- Adler GH, Levins R. 1994. The island syndrome in rodent populations. *Quarterly Review of Biology* 69: 473–490.
- Aksu AE, Calon TJ, Hall J, Mansfield S, Yaşar D. 2005. The Cilicia–Adana Basin complex, Eastern Mediterranean: Neogene evolution of an active fore-arc basin in an obliquely convergent margin. *Marine Geology* 221: 121–159.
- Ali JR, Huber M. 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463: 653–656.
- Anderson RP, Handley CO Jr. 2002. Dwarfism in insular sloths: Biogeography, selection, and evolutionary rate. *Evolution* 56: 1045–1058.
- Barnosky AD, ed. 2004. Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado. University of California Press.
- Barton NH, Turelli M. 2011. Spatial waves of advance with bistable dynamics: Cytoplasmic and genetic analogues of Allee effects. *American Naturalist* 178: E48–E75.
- Bowman RI, Berson M, Leviton AE. 1983. Patterns of Evolution in Galapagos Organisms. American Association for the Advancement of Science.
- Brown D. 2005. Secretary Island Deer Eradication. Southland Conservancy, New Zealand Department of Conservation.
- Brown JH. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *American Naturalist* 105: 467–478.
- Calder WA III. 1984. Size, Function, and Life History. Harvard University Press.
- Coughlin BL, Fish FE. 2009. Hippopotamus underwater locomotion: Reduced gravity movements for a massive mammal. *Journal of Mammalogy* 90: 675–679.
- Courchamp F, Chapuis J-L, Pascal M. 2003. Mammal invaders on islands: Impact, control and control impact. *Biological Reviews* 78: 347–383.
- Croizat L. 1958. Panbiogeography. Published by the author.
- Darwin C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray.
- Dermitzakis MD, Sondaar PY. 1978. The importance of fossil mammals in reconstructing palaeogeography with special reference to the Pleistocene Aegean Archipelago. *Annales Géologiques des Pays Helléniques* 29: 808–840.
- De Vos J, van den Hoek Ostende LW, van den Bergh GD. 2007. Patterns in insular evolution of mammals: A key to island palaeogeography.

- Pages 315–345 in Renema W, ed. *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Springer.
- Diamond JM. 1975. Assembly of species communities. Pages 342–444 in Cody ML, Diamond JM, eds. *Ecology and Evolution of Communities*. Harvard University Press.
- Eltringham SK. 1999. *The Hippos: Natural History and Conservation*. Poyer.
- Fisher RE, Scott KM, Naples VL. 2007. Forelimb myology of the pygmy hippopotamus (*Choeropsis liberiensis*). *Anatomical Record* 290: 673–693.
- Fritts EI. 2007. Wildlife and People at Risk: A Plan to Keep Rats out of Alaska. Alaska Department of Fish and Game.
- Grande L. 1990. Vicariance biogeography. Pages 448–451 in Briggs DEG, Crowther PR, eds. *Paleobiology: A Synthesis*. Blackwell Scientific.
- Grehan J. 2001. Biogeography and evolution of the Galapagos: Integration of the biological and geological evidence. *Biological Journal of the Linnean Society* 74: 267–287.
- Held SO. 1989. Early Prehistoric Islands Archaeology in Cyprus: Configurations of Formative Culture Growth from the Pleistocene–Holocene Boundary to the Mid-3rd Millennium B.C. PhD dissertation. University College, London.
- Hofmann RR. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia* 78: 443–457.
- Holden JC, Dietz RS. 1972. Galapagos Gore, NazCoPac Triple Junction and Carnegie/Cocos Ridges. *Nature* 235: 266–269.
- Jackson G, Gartlan JS. 1965. The flora and fauna of Lolui Island, Lake Victoria: A study of vegetation, men and monkeys. *Journal of Ecology* 53: 573–597.
- Johnson DL. 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *Journal of Biogeography* 7: 383–398.
- Kidwell SM, Behrensmeyer AK. 1993. Taphonomic Approaches to Time Resolution in Fossil Assemblages. *Short Courses in Paleontology*, vol. 6. Paleontological Society.
- Kidwell SM, Holland SM. 2002. The quality of the fossil record: Implications for evolutionary analyses. *Annual Review of Ecology and Systematics* 33: 561–588.
- Lawlor TE. 1986. Comparative biogeography of mammals on islands. *Biological Journal of the Linnean Society* 28: 99–125.
- Ledón-Rettig CC, Richards CL, Martin LB. 2013. A place for behavior in ecological epigenetics. *Behavioral Ecology* 24: 329–330.
- Lomolino MV, Riddle BR, Whittaker RJ, Brown JH. 2010. *Biogeography*, 4th ed. Sinauer.
- Lyman RL. 1994. *Vertebrate Taphonomy*. Cambridge University Press.
- McKenna MC. 1973. Sweepstakes, filters, corridors, Noah's arks, and beached viking funeral ships in palaeogeography. Pages 295–308 in Tarling DH, Runcorn SK, eds. *Implications of Continental Drift to the Earth Sciences*, vol. 1. Academic Press.
- McKinney ML, Lockwood JL, Frederick DR. 1996. Does ecosystem and evolutionary stability include rare species? *Palaeogeography, Palaeoclimatology, Palaeoecology* 127: 191–207.
- McNab BK. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. *American Naturalist* 144: 643–660.
- Marquet PA, Taper ML. 1998. On size and area: Patterns in body size extremes across landmasses. *Evolutionary Ecology* 12: 127–139.
- Marra AC. 2005. Pleistocene mammals of Mediterranean islands. *Quaternary International* 129: 5–14.
- Masini F, Bonfiglio L, Abbazzi L, Delfino M, Fanfani F, Ferretti M, Kotsakis A, Petruso D, Marra AC, Torre D. 2002. Vertebrate assemblages of central-western Mediterranean islands during the Pliocene and Quaternary: Reflecting on extinction events. Pages 437–444 in Waldren WH, Ensenyat JA, eds. *World Islands in Prehistory: International Insular Investigations*. Archeopress.
- Masseti M. 1995. Quaternary biogeography of the Mustelidae family on the Mediterranean islands. *Hystrix* 7: 17–34.
- . 2002. Uomini e (Non Solo) Topi: Gli Animali Domestici e la Fauna Antropocora. Florence University Press.
- Masters JC, Lovegrove BG, de Wit MJ. 2007. Eyes wide shut: Can hypo-metabolism really explain the primate colonization of Madagascar? *Journal of Biogeography* 34: 31–37.
- Masuda R, Yoshida MC. 1995. Two Japanese wildcats, the Tsushima cat and the Iriomote cat, show the same mitochondrial DNA lineage as the leopard cat *Felis bengalensis*. *Zoological Science* 12: 655–659.
- Matthew WD. 1939. *Climate and Evolution*, 2nd ed. Special Publications of the New York Academy of Sciences.
- Mayr E. 1942. *Systematics and the Origin of Species: From the Viewpoint of a Zoologist*. Columbia University Press.
- McNitt JJ, Patton NM, Lukefahr SD, Cheeke PR. 2000. *Rabbit Production*, 8th ed. Interstate.
- Meiri S. 2007. Size evolution in island lizards. *Global Ecology and Biogeography* 16: 702–708.
- Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF. 2005. The Phanerozoic record of global sea-level change. *Science* 310: 1293–1298.
- Millien V, Damuth J. 2004. Climate change and size evolution in an island rodent species: New perspectives on the island rule. *Evolution* 58: 1353–1360.
- Moore GS. 2007. *Living with the Earth: Concepts in Environmental Health Science*, 3rd ed. Lewis.
- Oliver WLR, Cox CR, Groves CP. 1993. The Philippine Warty Pigs (*Sus philippensis* and *S. cebifrons*). Pages 145–154 in Oliver WLR, ed. *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan*. International Union for Conservation of Nature.
- O'Regan HJ, Turner A, Wilkinson DM. 2002. European Quaternary refugia: A factor in large carnivore extinction? *Journal of Quaternary Science* 17: 789–795.
- Palombo MR. 2009a. Biochronology, palaeobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integrative Zoology* 4: 367–386.
- . 2009b. Body size structure of Pleistocene mammalian communities: What support is there for the “island rule”? *Integrative Zoology* 4: 341–356.
- Prescott JH. 1959. Rafting of jack rabbit on kelp. *Journal of Mammalogy* 40: 443–444.
- Pulquério MJF, Nichols RA. 2007. Dates from the molecular clock: How wrong can we be? *Trends in Ecology and Evolution* 22: 180–184.
- Raia P, Meiri S. 2006. The island rule in large mammals: Paleontology meets ecology. *Evolution* 60: 1731–1742.
- Raup DM. 1976. Species diversity in the Phanerozoic: An interpretation. *Paleobiology* 2: 289–297.
- Reed DH, O'Grady JJ, Brook BW, Ballou JD, Frankham R. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* 113: 23–34.
- Russell JC, Clout MN. 2005. Rodent incursions on New Zealand islands. Pages 324–330 in Parkes J, Statham M, Edwards G, eds. *Proceedings of the 13th Australasian Vertebrate Pest Conference*. Landcare Research.
- Sarnthein M, Bartoli G, Prange M, Schmittner A, Schneider B, Weinelt M, Andersen N, Garbe-Schönberg D. 2009. Mid-Pliocene shifts in ocean overturning circulation and the onset of Quaternary-style climates. *Climate of the Past* 5: 269–283.
- Severinghaus CW, Cheatum EL. 1956. Life and times of the white-tailed deer. Pages 57–186 in Taylor WP, ed. *The Deer of North America*. Wildlife Management Institute.
- Simpson GG. 1940. Mammals and land bridges. *Journal of the Washington Academy of Sciences* 30: 137–163.
- Stankiewicz J, Thiart C, Masters JC, de Wit MJ. 2006. Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals. *Journal of Biogeography* 33: 221–235.
- Stephens PA, Sutherland WJ, Freckleton RP. 1999. What is the Allee effect? *Oikos* 87: 185–190.
- Terborgh J. 1974. Preservation of natural diversity: The problem of extinction prone species. *BioScience* 24: 715–722.

- Thiede J. 1978. A glacial Mediterranean. *Nature* 276: 680–683.
- Van den Hoek Ostende LW, Meijer HJM, van der Geer AAE. 2009. A bridge too far. Comment on “Processes of island colonization by Oligo-Miocene land mammals in the central Mediterranean: New data from Scontrone (Abruzzo, Central Italy) and Gargano (Apulia, Southern Italy)” by P. P. A. Mazza and M. Rustioni [Palaeogeography, Palaeoclimatology, Palaeoecology 267 (2008) 208–215]. *Palaeogeography, Palaeoclimatology, Palaeoecology* 279: 128–130.
- Van der Geer A, Lyras G, de Vos J, Dermitzakis M[D]. 2010. *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands*. Wiley-Blackwell.
- Van Duzer C. 2004. *Floating Islands: A Global Bibliography*. Cantor Press.
- Van Valen LM. 1973. Pattern and the balance of nature. *Evolutionary Theory* 1: 31–49.
- Vigne J-D, Marinval-Vigne M-C. 1988. Contribution à la connaissance du cerf de Corse (*Cervus elaphus*, Artiodactyla, Mammalia) et de son histoire. *Bulletin d'Écologie* 19: 177–187.
- Wallace AR. 1869. *The Malay Archipelago—The land of the orang-utan and the bird of paradise: A narrative of travel with studies of man and nature*. Macmillan.
- Warren BH, Strasberg D, Bruggeman JH, Prys-Jones RP, Thébaud C. 2010. Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics* 26: 526–538.
- West JB. 2001. Snorkel breathing in the elephant explains the unique anatomy of its pleura. *Respiratory Physiology* 126: 1–8.

---

*Paul P. A. Mazza (paul.mazza@unifi.it) is affiliated with the Department of Earth Sciences at the University of Florence, Italy. Sandro Lovari is affiliated with the Department of Life Sciences at the University of Siena, Italy. Federico Masini is affiliated with the Department of Earth and Sea Sciences at the University of Palermo, Italy. Marco Masseti is affiliated with the Leo Pardi Department of Evolutionary Biology at the University of Florence. Marco Rustioni is affiliated with the Museum of Paleontology in Montevarchi, Italy.*