

The island immaturity – speciation pulse model of island evolution: an alternative to the “diversity begets diversity” model

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Islands have long provided model systems in which ecologists and evolutionary biologists have developed, tested and refined models for species diversity (Whittaker and Fernández-Palacios 2007). In two recent papers, Emerson and Kolm (2005a, b) have presented and discussed multiple regression analyses from two oceanic archipelagos, the Canaries and Hawaii, demonstrating for plants and arthropods that islands of greater species richness also have higher proportions of single island endemics (SIEs). They claim this as evidence that higher species richness of a taxon drives higher rates of diversification in that taxon, i.e. that “diversity begets diversity”. Their analysis is interesting, but given that it is an analysis of proportions of SIEs not rate of species production, it is ultimately inconclusive as to mechanisms leading to the relationship. It might tell us, as inferred by Emerson and Kolm (2005a, b), that high species richness creates the conditions for high rates of speciation through: 1) competitive interactions, 2) genetic drift due to small population sizes, and 3) greater community structural complexity. But it could also be that the relationship is a by-product of circumstances not adequately captured in their analyses.

Herein, we develop an alternative model, positing that the opportunities for speciation have a broadly predictable relationship to the life cycle of oceanic islands. We term our model the island immaturity – speciation pulse (IISP) model of island evolution. Intrinsic to this model is that opportunity drives speciation rate and that opportunity is greatest at a

relatively early stage of an island’s life cycle, when intrinsic carrying capacity exceeds species richness by the greatest margin, i.e. when there is greatest “vacant niche space”. As islands mature, both richness and endemism increase in tandem, but as islands decline in their old age, opportunities for speciation diminish, in tandem with a reduced carrying capacity (and reduced numbers of SIEs). Our argument is that the mechanisms identified by Emerson and Kolm (2005a, b), whilst each having a role in island evolution, make for an incomplete set of key island mechanisms and that in particular they neglect the likely importance of competitive release early in the life cycle of an island, and of the subsequent decline in carrying capacity, for the proportions of single island endemics (see Peck et al. 1999).

In setting out the IISP model, we describe the observations on which it is based, and then examine what we expect in terms of critical rates, and emergent patterns of SIEs, comparing our model with that put forward by Emerson and Kolm (2005a, b). We illustrate our model with reference to data for the arthropods and plants of the Canary Islands (cf. Emerson and Kolm 2005a).

Prior observations

First, numerous analyses of species richness variation provide broad support for the idea of an environmentally-determined carrying capacity (K) for richness on

islands (MacArthur and Wilson 1967, Wright 1983, Wylie and Currie 1993, Kalmar and Currie 2006). Notwithstanding, many oceanic islands fail to attain their hypothetical carrying capacity as they are too young or have had too little time since some past disturbance event(s) in which to rebuild their diversity (MacArthur and Wilson 1967, Paulay 1994, Peck et al. 1999, Heaney 2000, Lomolino and Brown 2000).

Secondly, setting aside the historical phase of anthropogenic species movements, remote islands receive colonists so rarely that immigration and speciation occur on similar timescales. Small, low-lying islands provide only a limited array of habitats, and are typically dominated by widespread strand-line species; hence, the highest proportions of island endemics occur on remote, large, topographically complex islands, especially those that are close to the dispersal limits of a particular taxon (the radiation zone sensu MacArthur and Wilson 1967; see also: Heaney 2000, Whittaker and Fernández-Palacios 2007).

Thirdly, oceanic islands are typically relatively short-lived land masses, with a broadly predictable life-cycle. The two systems examined by Emerson and Kolm (2005a), Hawaii and the Canaries, differ geologically in several important respects, but have in common a very considerable variation in island age within the archipelago. Young oceanic islands are characterised by cycles of volcanic activity, spread over varying lengths of time depending on the geological context (Whittaker and Fernández-Palacios 2007). Volcanic activity in association with hotspots, or with fracture lines near plate margins, can build steep islands of very considerable altitude (4205 m Mauna Kea, Hawaii; 3718 m El Teide, Tenerife), which are prone to rapid erosional attrition and subsidence. As a consequence of the erosion thus generated and of structural weaknesses characteristic of their flanks, these oceanic islands are also prone to suffer catastrophic losses in mega-landslides (Carracedo et al. 1998, 1999, Canals et al. 2000). For example, El Hierro (Canaries) lost about half its land mass in the El Golfo slide ca 15 000 BP (Carracedo et al. 1999). Over time, their eruptive activity slows, and whilst erosion then dominates, once their elevational range declines below ca 1000 m, catastrophic losses in area due to mega-landslides become less likely (Hürlimann et al. 2004). Therefore, the attrition of the island may slow as the island attains old age. Their eventual fate is to slip back into the sea, or, in tropical seas, to persist as atolls.

Fourthly, previous workers have commented that rates of species formation may vary through time on oceanic islands and specifically that speciation may occur at a greater rate early in the life of an island. For instance, in their analyses of picture-wing *Drosophila* on Hawaii, Kaneshiro et al. (1995, p. 71) conclude: “Most of these species, like many other extant terrestrial

endemic fauna, show a very strong but by no means exclusive tendency to single-island endemism. Most species . . . appear to evolve on an island early in its history and thereafter remain confined to that island. Colonists arriving at newer emerging islands tend to form new species . . .”. A similar conclusion was reached by Crawford et al. (1992) in a study of the endemic genus *Robinsonia* (Asteraceae) on Masatierra Island (Juan Fernández archipelago). Furthermore, Silvertown (2004) notes that within the Canarian flora, most large endemic groups (including spectacular case of adaptive radiation) are monophyletic. Silvertown (2004) argues that this is best accounted for via niche pre-emption mechanisms (Silvertown et al. 2005). If these arguments hold true, they point to opportunities for speciation being greatest for early colonists, especially for early and “lonely” colonists (those that are the only members of their lineage).

The island immaturity – speciation pulse model

We now combine the above observations and translate the ideas into the key island biogeographical parameters considered both by MacArthur and Wilson (1967) and by Emerson and Kolm (2005a, b): like them, illustrating our model in a simple graphic (Fig. 1). For comparison with Emerson and Kolm, we consider also the implications of the island immaturity – speciation pulse (IISP) model for the proportions of single island endemics (SIEs).

The carrying capacity of oceanic islands is, to a first approximation, a function of the area and elevational range, providing climate is controlled for (Kalmar and Currie 2006). As described above, the hypothetical carrying capacity of a volcanic island over the course of its existence can be predicted to increase from zero to a maximum when the island is at greatest extent and elevational range, declining thereafter until submergence. A smooth hump-shaped trend in carrying capacity would thus be expected, but should be seen as hypothetical. Violent volcanic activity during the active phase, and catastrophic landslides during the middle-age of the island, may cause sudden temporary or permanent (respectively) declines in carrying capacity, thus in practice producing a rather more complex trend in K , superimposed on the general hump-shaped pattern.

Species immigration I to a new oceanic island will be dominated by colonists from other islands within the group, but due to the isolation of the islands is assumed to occur at a fairly low rate, reducing further over time once the more dispersive species of the archipelago pool have colonized. Hence, the species richness R will climb, but will not be capable of reaching the hypothetical

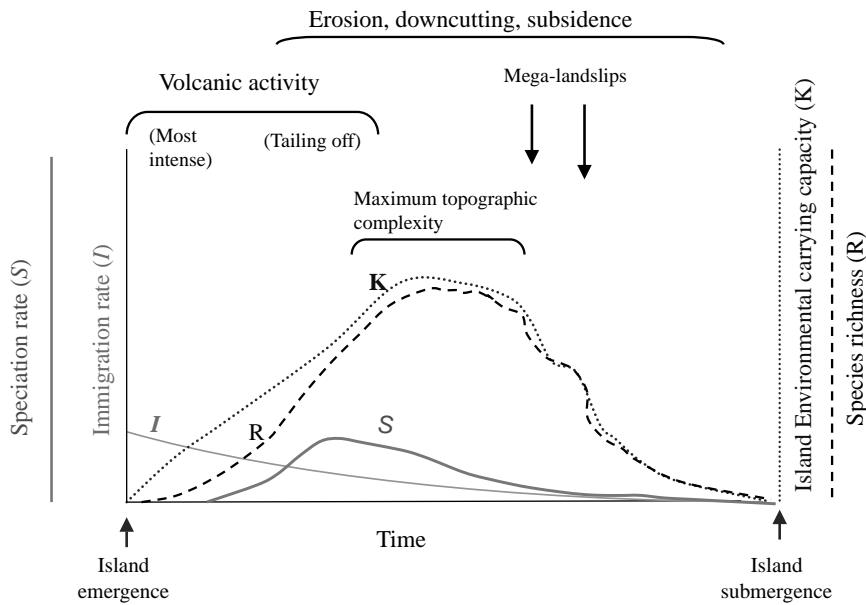


Fig. 1. The island immaturity – speciation pulse model of island evolution, showing the form of variation expected in species richness (R), the intrinsic carrying capacity of the island (K), immigration rate (I) and speciation rate (S). The greatest opportunities for speciation (i.e. where the gap between R and K is greatest) are when an intermediate number of the eventual colonist lineages have arrived, and where environmental complexity is great. This is likely to occur not in extreme youth, but during the youth of the island nonetheless, with opportunities for adaptive radiation greatest in this phase. At the very earliest stage of island colonization, increasing R is driven by I (mostly from older islands within the archipelago), but the rate of I declines (as per MacArthur and Wilson 1967) as R increases and the proportion of the archipelagic pool already on the island increases. Speciation takes time, and so the rate of speciation lags slightly behind the increased “opportunity” ($\equiv K-R$), increasing to a peak early on in the islands’ history and then slowly declining. The amplitude of I and S curves may vary as a function of effective isolation (compare with Heaney 2000, Fig. 5). Later speciation events, during the old age of an island, are more likely to be consistent with the anagenesis model (Stuessy et al. 1998, 2006) than is the case on younger islands. For discussion of extinction rate (E) variation, see text.

carrying capacity K via immigration alone without the lapse of an unrealistically long period of time.

Opportunities for phylogenesis (indicated by maximal values of $K-R$), and especially for adaptive radiation, can thus be expected to be greatest at a fairly early stage in the process of biotic accumulation on a remote island, when there are sufficiently complete ecological systems to provide adaptive opportunities, but still plenty of “unoccupied” niches. As opportunity allows, so speciation is initiated, and the rate of production of single island endemics (SIEs) increases to a peak at a comparatively early stage. This will occur by a variety of mechanisms, as island evolution results from a combination of sympatric, parapatric and allopatric mechanisms (Wagner and Funk 1995, Emerson 2002, Savolainen et al. 2006, Whittaker and Fernández-Palacios 2007), producing new species both by anagenesis and cladogenesis. As the island ages, the complex eruptive and erosive history of the evolutionary platform may provide additional opportunities for non-adaptive radiation by within-island isolation (vicariance

or peripheral isolation) within the dissected and complex island landscape (Carson et al. 1990).

From this point in the island’s history, we can consider two scenarios (using the notation in Fig. 1, and with E = extinction rate): 1) as R gradually approaches the fixed K value, S should decline even as R continues to increase. 2) If the notion of a fixed K is considered an illusory concept (because increasing diversity allows more diversity to evolve, as Emerson and Kolm 2005a), then S must still eventually fall with the decline and submergence of the island itself. At this stage however fast evolution may be working, K is diminishing (Stuessy et al. 1998), and so $E > (I+S)$ and the inevitable slide back into the ocean will necessarily draw R (and with it S) down to zero. Hence, we expect to find that the relative contribution of I and S to the richness of a remote island will vary through time as shown in Fig. 1. Further, whilst both S and I may each decline during the phase of island subsidence/destruction, the relative importance of S may be greater than in the very earliest stages (thousands of years) of the island’s history, during which (as argued by

Heaney 2000) most of the increase in richness comes from immigration.

To complete the model, we must consider the loss of SIEs in a little more detail. This can occur through two mechanisms: 1) colonizing another island, or 2) simply going extinct.

1) Colonizing another island: when islands exist for lengthy periods, opportunities exist for some of their new endemics to island hop to other, younger islands, thus becoming (at least for a while) a multiple-island endemic and no longer an SIE. Many more lineages follow such a “progression rule” than back-colonize (Funk and Wagner 1995, Stuessy et al. 1998).

2) Extinction: we have not attempted to sketch an extinction rate curve in Fig. 1, but we anticipate that in terms of biotic drivers of extinction, E should initially be extremely low, but increase as R approaches K, whilst remaining very low in absolute terms. However, these biotic drivers of extinction are likely to be dwarfed by abiotic drivers; at early stages by mega-disturbance phenomena (damaging eruptions, mega-landslides), in the later stages of the island life cycle by the gradual attrition of topographic relief and area (Stuessy et al. 1998, Peck et al. 1999), and over the last 10 000 yr, by “relaxation” associated with the loss of area due to post-glacial sea-level rise.

Over the life-cycle of an island as sketched in Fig. 1, we would therefore anticipate that in extreme youth $I > S > E$, from youth towards island maturity $S > I > E$, interrupted by phases of high E (catastrophe), and that in advanced old age, $E > (S + I)$, with similarly low rates of S and I pertaining. The attrition of numbers of species of SIE status within the biota through the progression rule, and through the loss of specialist interior (especially upland) habitats through erosional attrition, should result in a decline in both the number and the proportion of SIEs on the oldest islands. An example of the “erosion-driven loss” line of argument is provided by Emerson and Oromi (2005) in their discussion of the forest beetle genus *Tarphius* from the Canary Islands: “The oldest islands of Fuerteventura and Lanzarote are inhospitable to *Tarphius* species due to their lack of suitable humid habitats. However, it is highly likely that humid habitats occurred on these two islands before they reached their current state of erosional degradation, and that these would have contained species of *Tarphius*.” This argument, if valid for *Tarphius*, presumably could apply to numerous other forest lineages.

Evaluation ~ applicability to the Canaries

The foregoing line of argument applies to the life cycle of a single island within an archipelago. Unfortunately,

we are unable to wait millions of years to test this. One way of exploring the validity of the model is therefore to use ergodic reasoning (space-for-time substitution). Applying the IISP model to an archipelago with a sufficiently complete range of island ages, we expect to see a humped relationship between speciation rate and island age, and ~ because of the expected attrition of SIEs on older islands ~ a humped relationship between the proportion of SIEs and island age. We lack the data to test the first of these expectations for more than a handful of lineages, but we can examine the second proposition.

We must acknowledge that applying space-for-time substitution to the Canaries is problematic. First, although the age of origin of each of the islands is more or less agreed upon, volcanic activity may have had a huge island-specific influence on their carrying capacity through time. For example, some 3.5 Ma, the catastrophic Roque Nublo ash flow is thought to have almost completely sterilized the island of Gran Canaria (Marrero and Francisco-Ortega 2001, Emerson 2003). Recolonization then followed from the other islands. Second, the two oldest islands of the Canaries, Lanzarote and Fuerteventura, were joined together into a single large island (Mahan, ca 5 000 km² in area) at the peak of the last Ice Age, and have thus once again become separate islands only within the last 10 000 yr. Third, the modern island of Tenerife is composed of three Tertiary age massifs (oldest date 8 Ma), which were fused together to form a single island only within the last 2 million years. However, some 10% of the endemic plants of the Canaries are restricted to one or more of the three palaeo-islands (Trusty et al. 2005), suggesting continuity of at least some lineages from these early massifs. Hence, we assume an age of 8 Ma. From these three examples, we can see that the development of the archipelago has seen a complex geological dance where islands rise, fall, merge, split, and are periodically incinerated. Nonetheless, we follow Emerson and Kolm (2005a) in using island age as derived from recent geological data (specifically, we used Carracedo et al. 2002), acknowledging the Roque Nublo event by using an age of ca 3.5 Ma for Gran Canaria (as Emerson 2003) instead of 14 Ma.

Figure 2 plots the proportion of single island endemics (PSIE) in arthropods and plants, using data from the most recent compilation of Canarian fauna and flora (Izquierdo et al. 2004). The trend shown in each data set appears consistent with the expectations of the IISP model that the proportion of single island endemics should show a humped pattern with island age. The limitations in the use of ergodic reasoning and the close attention of five reviewers, prohibit us from claiming this as a critical test, but let us assume for the moment that it is a valid strand of evidence.

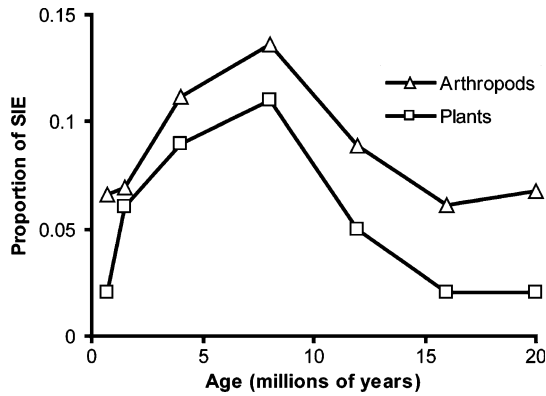


Fig. 2. The relationships between island age and the proportions of single island endemic species (PSIE) for arthropods and for higher plants for the seven main Canary Islands (data from Carracedo et al. 2002, Izquierdo et al. 2004). The age of Gran Canaria is given as 3.5 Ma, allowing for its sterilization in the Roque Nublo ash flow (see text). NB. Were the data for the oldest two islands, Lanzarote and Fuerteventura combined, to represent the late-glacial period island of Mahan (see text), the form of the curve would remain hump-shaped.

How consistent is this pattern with the “diversity begets diversity” argumentation of Emerson and Kolm (2005a, b)?

Emerson and Kolm (2005a, b) pay relatively little attention to island age, which is eliminated as a variable in their analyses of Canarian plants and arthropods because (as Fig. 2 shows) it is not linearly related to PSIE. However, Emerson and Kolm (2005b) do make an explicit prediction about how PSIE should vary with island area in the context of an island at equilibrium. They argue that “for two islands with a similar colonization rate but having different numbers of species because of their different sizes, the smaller island . . . should have a greater proportion of endemic species than the larger island.” This is because Emerson and Kolm (2005a, b) place emphasis on competitive mechanisms, arguing that smaller average population sizes fuel both increased extinction and increased speciation: with the rates of both varying in tandem. Hence, applying their logic (Fig. 1 of Emerson and Kolm 2005b) to the scenario of older islands losing area, generates the expectation that under dynamic equilibrium conditions (which they argue applies for instance to Canarian arthropods) reduction of area through time would lead to reduced richness but increased proportions of endemic species (Emerson and Kolm 2005b).

Emerson and Kolm (2005b) argue that the prediction of smaller islands having a greater proportion of endemic species than larger islands is derivable from MacArthur and Wilson’s (1967) island theory.

However, MacArthur and Wilson (1967, p. 173) state that “. . . on both theoretical and empirical grounds . . . the turnover rates of species varies inversely with island area. It follows that the percentage endemism should increase with island area.” This appears to be in direct opposition to the passage from Emerson and Kolm (2005b) quoted in the previous paragraph. It therefore appears to us that the strong positive linkage claimed between the behaviour of extinction and speciation rates is not derivable from MacArthur and Wilson (1967). Rather, MacArthur and Wilson (1967, e.g. pp. 173–175) argue that cladogenesis is greatest in remote archipelagos, and that as species formation via anagenesis requires lengthy time periods, it is favoured by low turnover (thus low E), i.e. by large island size: hence summing to large remote islands and archipelagos having greatest percentage endemism. Moreover, if Emerson and Kolm’s reasoning is correct, then a small atoll should have a higher proportion of single island endemics on it than the big island of Hawaii, providing it has an equivalent degree of isolation. This prediction is not supported (Mayr 1965, MacArthur and Wilson 1967). Note also that neither of the two passages cited above considers an island age – island size (and carrying capacity) relationship of the form discussed herein.

We have acknowledged above that the precise form of the trend shown in Fig. 2 is subject to assumptions made about island ages, but whatever the precise form of these relationships, it is clear that the proportions of endemics are not highest on the oldest islands. If we look back to Emerson and Kolm’s (2005a) three mechanisms of diversification, viz: 1) competitive interactions, 2) genetic drift due to small population sizes, and 3) greater community structural complexity, if they are key to diversification in Canarian arthropods and plants, then it is odd that the operation of 1) and 2) on Lanzarote and Fuerteventura over so much longer a time span has not produced more diversification than on the younger islands. Hence, we conclude that Fig. 2 provides greater credence to mechanism 3), and to the importance of: 4) ecological release mechanisms (~vacant niche space), and 5) within island allopatry. This is consistent with the fact that the richer, intermediate-aged islands do have greater complexity of habitats, distributed across a greater array of major ecosystem types, arrayed across more steeply dissected topography, in comparison with the two oldest islands. And, it is on these younger islands, that opportunities for speciation and for single island endemics to evolve and survive to be counted have evidently been greatest in recent evolutionary time. Similar conclusions were drawn by Peck et al. (1999) in their analyses of species/genus ratios in Hawaiian insects. Hence, we suggest that the island immaturity – speciation

pulse model provides a plausible alternative to the “diversity – begets diversity” interpretation of Emerson and Kolm (2005a, b).

Unfortunately, the empirical evaluation of these ideas depends on several simplifying assumptions and on a necessarily small number of islands (each with a complex environmental history), making formal statistical analyses based on proportions of single island endemics largely intractable. The most profitable route to testing these alternative ideas and models would therefore seem to be via analyses of phylogenies of multiple taxa. In the meantime, whilst the proportion of single island endemics may indeed be correlated with species richness of the same taxa, this does not appear to be a satisfactory basis on which to base claims of causation for diversification rates and patterns for islands, or for that matter, why there are so many species in the tropics (Emerson and Kolm 2005a, p. 1017).

Acknowledgements – We thank Joaquín Hortal, Paulo Borges, Brent Emerson, Kostas Triantis, and Carsten Rahbek for insightful comments on a previous draft.

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