A unified model of island biogeography sheds light on the zone of radiation

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Abstract:

Islands acquire species through immigration and speciation. Models of island biogeography should capture both processes, however quantitative island biogeography theory has either neglected speciation or treated it unrealistically. We introduce a model where the dominance of immigration on small and near islands gives way to an increasing role for speciation as island area and isolation increase. We examine the contribution of immigration and speciation to the avifauna of 35 archipelagoes and find, consistent with our model, that the zone of radiation comprises two regions: endemic species diverged from mainland sister-species at intermediate isolation and from insular sister-species at higher levels of isolation. Our model also predicts species-area curves in accord with existing research and makes new predictions about species ages and abundances. We argue that a paucity of data and theory on species abundances on isolated islands highlights the need for island biogeography to be reconnected with mainstream ecology.

Introduction

The colonisation of Krakatau and evolution of species on the Galápagos exemplify two ways in which island biogeography has captured the imagination of ecologists and evolutionary biologists alike. Islands have played a unique role in ecology and evolution, both as an inspiration for new ideas (Darwin 1859; Mayr 1954; MacArthur & Wilson 1963) and as natural laboratories whereupon theory can be tested (Whittaker & Fernández-Palacios 2007). No island-inspired ecological theory has left a greater legacy than MacArthur and Wilson's equilibrium theory of island biogeography (MacArthur & Wilson 1963, 1967; Losos & Ricklefs 2010), which predicts species richness and turnover on islands as an emergent equilibrium between immigration and extinction. MacArthur and Wilson observed that on sufficiently isolated islands speciation may come to influence diversity and they referred to this as the "zone of radiation". However, their equilibrium model did not include speciation and was not intended to be applied in this context (MacArthur & Wilson 1963, 1967). More recent quantitative theories have extended MacArthur and Wilson's theory to include speciation (Johnson *et al.* 2000; Chen & He 2009), but they have not allowed for different routes to speciation and have made limited community level predictions. The remaining models for species richness on remote islands are verbal only (Ricklefs & Cox 1972; Heaney 2000; Stuessy 2007; Whittaker *et al.* 2008).

There are two geographic modes of speciation on an island, either an island population may become reproductively isolated from the mainland source population (anagenesis), or two island populations may become reproductively isolated from each other *in situ* (cladogenesis). Anagenesis replaces immigrant species with endemics and thus does not increase the species richness on the island, but does increase global diversity. Cladogenesis, in comparison, increases both island species richness and global diversity. We use the term endemic to refer to species that are unique to an island irrespective of the cause for the uniqueness, which could be anagenesis or cladogenesis. The increasing availability of phylogenetic data for island taxa (Gillespie 2004) makes it possible to identify the geographical whereabouts of endemic species' sister taxa (Heaney 2000; Kisel & Barraclough 2010). We refer to an endemic species whose sister is found elsewhere as anagenetic and an endemic species whose sister is found on the same island as cladogenetic. It is probable that anagenesis leads to an anagenetic species and cladogenesis to cladogenetic species. However, pattern does not always reveal process, for example, if one of a pair of cladogenetic species goes extinct anagenesis would falsely be inferred (see supporting information).

The species abundance distribution is one of the most-studied patterns in ecology and was discussed at length by MacArthur and Wilson (1967). Nonetheless, their equilibrium model makes no direct predictions about the form of abundance distributions. Perhaps as a consequence, species abundances have received much less attention from island biogeographers than species richness and turnover (but see Mayr & Diamond 2001), both of which are predicted under MacArthur and Wilson's model. The unified neutral theory of biodiversity and biogeography (Hubbell 2001) builds on the theory of island biogeography, but models the abundances of species at the individual level. It was conceived as a general theory for a "local community`' patch, receiving immigrants from a "metacommunity" species pool. The majority of work interprets the "local community" as a spatial sample from the mainland despite the great potential for island biogeography applications (Hubbell 2010). Speciation in classic neutral theory is by "point mutation" where new species arise spontaneously as singletons in the meta-community. There is no speciation in the local community (island) under the classic model (but see Hu *et al.* 2007): this can usually be justified as the theory tends to be applied to small local communities with high turnover where speciation can be ignored. However, ignoring speciation limits the theory's usefulness in the context of island biogeography, where island endemics exist and are often of particular interest.

Here we present a new unified model that mirrors observed patterns of endemism on islands; it predicts the richness, age and abundances of species on islands and incorporates speciation via both anagenesis and cladogenesis. We collated a worldwide phylogenetic dataset for avifauna across a range of islands and archipelagoes, producing results consistent with our model's predictions, but which are not addressed by MacArthur and Wilson's (1967) theory. Our model predicts a threshold island size for cladogenesis and a large effect of isolation on speciation, with intermediate levels of isolation promoting the most anagenesis. Species-area curves for endemic species are steeper than those for all species when immigration rate is proportional to island coastline. We also make novel predictions about species ages and abundances, for example, that in natural systems single island endemic species are expected to be relatively abundant. Despite the potential for species abundance data from island systems to inform us about the dominant processes involved in island biogeography, there is currently an unfortunate paucity of data.

Methods

An individual based model

We propose an individual based model based on ecological neutral theory (Hubbell 2001), thereby enabling us to predict a wide-range of phenomena, including species abundance distributions. Our model incorporates a mainland species pool with a species abundance distribution that can be freely varied to reflect empirical data or the predictions of any model of mainland species abundances. We explore three possible mainland species abundance distributions: difference log series (Rosindell *et al.* 2010), log series and uniform. Since the mainland only acts as a source of immigrants to the island, we could interpret the "abundances" of species on the mainland as being the product of abundance and relative dispersal ability.

Individual organisms die in the model at a constant rate, thus species' populations can dwindle and become extinct via the process of ecological drift. The smaller the population size, the greater the probability of imminent extinction. With every death of an individual on the island, a gap opens. With probability $1-m$ this gap will be filled by offspring from another living individual on the island, and with probability m the gap will be filled by an immigrant (Fig. 1). The flux of immigrants for fixed m would be proportional to island size J (measured in number of individuals). We also experiment with $m \propto \sqrt{J}$, making immigration proportional to the width of the island from an immigrant eye perspective.

Speciation in our model is not "point mutation" as employed by classic neutral theory (Hubbell 2001). Point mutation speciation founds all species with a single individual, which is in itself unrealistic and also leads to unrealistically high rates of species turnover (Rosindell *et al.* 2010). We model two distinct modes of speciation: anagenesis and cladogenesis and we introduce greater realism and complexity beyond the point mutation process. First, speciation takes time. Second, founding abundances of species are greater than one. Third, gene flow with mainland populations impedes anagenetic speciation. Our aim is to find a parsimonious model to explain empirical and qualitative patterns; we therefore chose to model the important emergent behavior of more complex genetic processes without including the genetics explicitly.

To model cladogenesis, we use a version of "protracted speciation" (Rosindell *et al.* 2010), under which speciation is a gradual process rather than an instantaneous event. "Variant" individuals appear at per capita rate κ and are each conspecific with their parent species. Note that these variant populations have also been referred to as "incipient species" arriving at rate μ in previous work (Rosindell *et al.* 2010). The probability κ of cladogenesis initiation is expected to be small; as this can be interpreted as implicitly encompassing the combined probabilities of a variant forming and overcoming gene flow's homogenizing influence on speciation. The arrival of a "variant" can be regarded as the stochastic selection of an individual that will later become a common ancestor to the complete population of the new species. Variants may give rise to offspring according to the usual rules of the model, if any offspring survive after a transition time of $\boldsymbol{\tau}$ generations has passed, then they are treated as a new species. One possible interpretation is that protracted speciation is simply a phenomenological way for new species to begin with founding abundances, picked according to a flexible distribution. It does not necessarily imply sympatric speciation within the island and is equally consistent with intra-island allopatric or parapatric speciation. Under protracted speciation, the initial population size of a new species is expected to be approximately $\boldsymbol{\tau}$ (Rosindell *et al.* 2010). As $\boldsymbol{\tau}$ increases, the distribution of founding abundances becomes flatter and closer to the alternative random fission model where a species is cleaved randomly in two new species (Haegeman & Etienne 2010; Rosindell *et al.* 2010). In the context of ecological neutral theory random fission speciation has been criticized just as much as point mutation speciation (Ricklefs 2003; Haegeman & Etienne 2010); and protracted speciation can be seen as a more realistic compromise between the two extremes (Rosindell *et al.* 2010).

Our model for anagenesis uses a novel implementation of the protracted speciation concept, inspired by genetic speciation models such as the Bateson-Dobzhansky-Muller model (Gavrilets 2004). The first immigrant of a mainland species to an island is always regarded as being a variant of the mainland population but is not yet an endemic species. If the island variant population survives for τ generations with no further immigration of conspecifics from the mainland, then it will be recognized as a new species. Prior to τ generations elapsing, every further conspecific immigrant joining the island population retards anagenesis by increasing the remaining time to speciation completion by G (a small predefined amount); in this way sufficiently high gene flow makes speciation near impossible. We never allow the remaining waiting time to speciation to be greater than τ. Completed speciation events cannot be reversed; once an island endemic is formed, further immigration of the mainland sister species will not affect it, but will instead form a new variant that can potentially become another endemic species (although this scenario rarely comes to pass).

In this paper we define immigrant species as those with conspecifics that exist on the mainland. Anagenetic and cladogenetic species are defined based on the pattern in the phylogenetic tree predicted by the model. The complete model is explained graphically in Fig. 1. We simulate the model using a coalescent procedure (Rosindell *et al.* 2008, see supplementary information).

Bird Richness There are few cases where the phylogeny of a community across multiple islands of varying size and isolation is known, *Bulimulus* snails on the Galapagos (Parent & Crespi 2006) and *Anolis* lizards in the Caribbean (Nicholson *et al.* 2004) are two notable exceptions. Here, we restrict our focus to birds, due to the availability of good quality data for both their phylogeny and geographic distribution. However, as birds appear not to speciate *in* *situ* on islands smaller than Jamaica (Coyne & Price 2000), we treat archipelagoes as islands and count the number of immigrant, anagenetic and cladogenetic species. Certain distributions of islands within archipelagoes are likely to facilitate within-archipelago cladogenesis better than others. In the context of our model this variation will affect parameter κ and thereby the rate of cladogenesis. This parameter could, for example, be set higher on archipelagoes with more islands per unit total area or where islands are more isolated from each other.

We compiled data on the avifauna of 35 islands and archipelagoes of varying size (14.2 – 36870 km^2) and isolation (11 – 4300 km) and lying in the latitudinal range -40° - 40° (Table S1). For an archipelago to be included it had to consist of islands in a cluster. The majority of information on island/archipelago land area, isolation (minimum distance, in km) from nearest continent and island number (the number of islands with area ≥ 10km^2) was obtained from the UNEP island directory (http://islands.unep.ch/isldir.htm). For some islands/archipelagoes a closer large island is a more probable source of colonists than the nearest continent. For instance, Mauritius and Reunion are more likely to be colonised from Madagascar than the African continent. In these cases we estimated isolation as the great circle distance to the presumed source island rather than to the continent.

For most islands/archipelagoes we compiled a list of resident non-introduced species using Avibase (http://avibase.bsc-eoc.org/). Species that are known to have gone extinct since humans colonised islands were also included, although this will tend to be an underestimate. For the Californian Channel Islands we used the species list reported by an earlier survey (Howell 1917) and for Hawaii we treated the honeycreeper radiation as including 50 species. We tried to ensure that the analyses were conducted across a single trophic level so that the results were comparable with the results of the neutral model; therefore, raptors, owls, water birds, kingfishers and seabirds were excluded. We also excluded rails due to evidence that insular forms have been particularly vulnerable to extinction (Steadman 2006). The remaining species comprise those feeding mainly on plants (seeds, fruits and nectar), invertebrates and a combination of the two.

Species that were not endemic to the archipelago were classed as immigrants. A species was classed as anagenetic if it was endemic to an archipelago but with a sister species/clade that is not endemic to the archipelago. A species was classed as cladogenetic if both it and its sister species/clade were endemic to the archipelago (note that this differs slightly from the definition of cladogenetic species under the simulation approach, where it is possible for only one of a species pair to be cladogenetic, see supplementary materials). Where multiple members of a genus were endemic to the archipelago, we tried to establish the relationships among them on the basis of phylogenetic studies and taxonomy (Dickinson 2003). In 17 cases there was insufficient evidence for us to establish whether species should be classed as anagenetic or cladogenetic and we excluded these from the analyses (note that results were qualitatively unchanged if these individuals were instead assigned as cladogenetic or anagenetic species)

We estimated the effect of area and isolation (both ln transformed) on the richness of i) immigrant, ii) anagenetic and iii) cladogenetic species, respectively using a generalized linear model with Poisson family errors in R (R Development Core Team 2010). Quasi-likelihood estimation was used to account for overdispersion. We first fitted a maximal model that included area, isolation and isolation^2. We then followed a stepwise deletion procedure, using *F* tests to compare model's residual deviance. We report the results from models from which any further deletion of terms would lead to a significant increase in residual deviance.

A strong positive correlation exists between archipelago area and the number of islands that make up the archipelago (Pearson's r = 0.71). To test whether the effects of island area on diversity arise due to area being a proxy for the number of islands, we included island number (ln transformed) as an additional term to our best models. If this term was a significant predictor of richness and changed the direction of the effect of area or rendered the effect of area non-significant, this would be consistent with area being a proxy for the number of islands and cast doubt on a direct effect of area on richness.

Results and Discussion

Species richness and endemicity

Our model predicts that the total number of species will decrease as island isolation increases (Fig. 2 A-C) due to lower immigration rates. This is consistent with empirical observations (Mayr 1965; Diamond 1972; Lack 1976) and the theory of island biogeography (MacArthur & Wilson 1963, 1967). In the limit of extreme isolation, species richness levels off at the number of species that can be sustained by cladogenesis alone, matching the predictions of earlier graphical models (Heaney 2000; Whittaker *et al.* 2008). It should be noted that, as with MacArthur and Wilson's equilibrium theory (MacArthur & Wilson 1963, 1967), we assume that the island is at ecological equilibrium, whereas, in reality, the most remote islands may either not have been colonised or not be at equilibrium (Whittaker 1995; Heaney 2000).

For small and remote islands, the model predicts a single anagenetic species. This is because if cladogenesis is initiated, the resulting variant will either become monodominant or extinct before the transition time τ has passed. The model's prediction for the relationship between species richness and area (species-area curve) on isolated islands therefore shows a clear area threshold below which no cladogenetic species will be seen (Fig. 2F). Although below this threshold our model predicts a single species only, this does not mean that the island is able to host only one species: neutral models apply to a single ecological guild and hence there would be one species per guild on the island when area is below the threshold for cladogenesis. In the cases where isolation is not so extreme, a cladogenesis threshold still exists in the model, but multiple immigrant and anagenetic species can be seen below this threshold, even within a single ecological guild (Fig 2. E,H).

It has been noted that the species-area curve for insular *Anolis* is shallow across the smallest islands, with one – three species being present, becoming much steeper once the island is larger than a threshold of 3000km^2 (Losos & Schluter 2000). The threshold is generally attributed to increased opportunities for vicariance and natural selection for adaptation to more diverse habitats on larger islands (Losos & Schluter 2000) or to the emergence of more beneficial mutations (Gavrilets & Vose 2005). A similar pattern emerges from our neutral model, where the per-capita probability of cladogenesis is fixed. Our finding is actually consistent with the work of Gavrilets and Vose (2005), where beneficial mutations leading to speciation arise more readily in larger populations.

Empirical species-area curves for single island endemics are generally steeper than those for more recent colonists (Ricklefs & Cox 1972; Ricklefs & Bermingham 2004) or all native species (including endemics) (Triantis *et al.* 2008). Our model can also reproduce these results: When there is a mixture of endemic and immigrant species, the full species-area curve is significantly shallower than the species-area curve for more isolated islands where endemics predominate, the latter being steep and close to unity when island size is sufficiently large, in line with empirical observations (Losos & Schluter 2000) (Fig. 2 H). Interestingly, this result is contingent on immigration rates that increase proportionally with island width rather than island area (Fig. 2 E,H). The species area curve predictions of the model are highly dependent on the degree of isolation, so that the species-area curve for islands closely linked to the mainland is similar to that expected if just sampling from the mainland (Fig 2. D). When immigration is proportional to island diameter, cladogenetic and anagenetic species start to be observed even when the island is not far from the mainland (Fig 2. G).

Immigrant and endemic island birds

In close agreement with predictions of our model and earlier empirical work (Mayr 1965; Adler 1992), the richness of different species types is heavily dependent on the isolation and area of archipelagoes and islands. Avian immigrant species richness correlates positively with area and negatively with isolation (Fig. 3A), which is consistent with the predictions of the simulation model (Figs. 2A-D, 3D). On all islands that are < 175km from a source pool more than 90% of species are classed as immigrants. For cladogenetic species, our statistical and simulation models agree in predicting richness to be highest on large and remote islands (Figs. 2 and 3). Indeed, we observed no avian cladogenetic species on archipelagoes < 175km from a source pool and a positive effect of area and isolation (Fig. 3C). A small discrepancy between the empirical data and our simulation model is that we found no evidence for numbers of cladogenetic bird species leveling-off as isolation increased. Possibly, the high levels of vagility among birds renders no archipelago sufficiently isolated for us to see the leveling-off predicted by our model (Fig. 2B,C). The anagenetic species richness of birds shows an increase with area, but the relationship between isolation and anagenetic species richness is hump-shaped, initially increasing then declining (Fig. 3B). This is in accord both with the simulation model predictions – where anagenetic species were also found to peak on islands of intermediate isolation (Fig. 2A-C) and increase with area – and earlier graphical models (Heaney 2000;

Whittaker *et al.* 2008). We postulate that the cause of the intermediate-hump is a trade-off between there being sufficient immigration to repeatedly initiate anagenesis but not so much that gene flow prevents speciation. All but one of the relationships described above were qualitatively unchanged when island number was included in the statistical analysis. The one qualitative change was that area becomes a marginally non-significant positive predictor of anagenetic species richness (b = 0.26±0.14 versus b = 0.32±0.08).

Species age and abundance

Our simulation model predicts the species abundance distributions for immigrant, cladogenetic and anagenetic species on islands across a range of levels of isolation (Fig. 4). We find that the least isolated islands are essentially samples of immigrants from the mainland, as isolation increases the abundance distribution becomes decoupled from the mainland (see supplementary material) and similar to that predicted by the standard neutral model (Hubbell 2001). Islands with intermediate levels of isolation contain a mix of immigrant, anagenetic and cladogenetic species, with the endemic species tending to be more abundant. Although there is a dearth of empirical research on the abundance distributions of insular taxa, some studies report patterns that fit with our predictions. For instance, Mayr and Diamond reported that Northern Melanesian birds show a positive correlation between species abundance and inter-island divergence into subspecies and allospecies (Mayr & Diamond 2001). However, Ricklefs and Bermingham (2002) found the opposite pattern for the West Indies avifauna, with endemic bird species being less abundant than immigrants; a non-neutral explanation for these data seems most likely. A study of insect and spider rarity on oceanic islands showed that endemic species, although rare in most habitats, are common in native forest (Borges *et* *al.* 2008), suggesting that human disturbance is one likely explanation for departures from our model's predictions.

If an island is sufficiently remote, our model predicts that most species will arise from cladogenetic radiations, because there is very low immigration and anagenetic species will tend to undergo cladogenesis (Fig. 4I). On such isolated islands abundances appear to be difference log-series distributed (Hubbell 2001; Rosindell *et al.* 2010). A difference log-series is the species abundance distribution expected from a neutral metacommunity with protracted speciation; for common species its prediction converges to that of the classic log-series, but the difference log-series has fewer rare species and an interior mode more like the log-normal distribution (Hubbell 2001).

The current leading theory predicting abundances of island endemics is the taxon cycle (Ricklefs & Cox 1978; Ricklefs & Bermingham 2002), of which several variants exist. Broadly speaking, however, species pass through the following stages under the taxon cycle: first immigration and an increase in abundance, then speciation into different allospecies on different islands, then range contraction and extinction, resulting in a patchy distribution of endemic species with some islands uninhabited by the taxon, after which some forms may expand their distribution initiating a new cycle. We anticipate that some patterns characteristic of taxon cycles will arise under our model; for instance, a species that had recently colonised would tend not to be endemic. Our model, or a spatially explicit archipelago version of it, has the potential to provide a null model for taxon cycles that may shed light on which empirical patterns require more complex non-neutral explanations.

Our model predicts that where endemic species exist they will tend to be old, with τ setting a minimum age (Fig. 5A-C) because age is counted back to the date speciation started and thus no species can possibly be younger than the time it took to speciate. In agreement with our predictions, genetic studies addressing island bird populations have revealed that larger and more isolated islands contain older populations, with these same islands also possessing more endemic species (Cadena *et al.* 2005; Price *et al.* 2010). We predict that the age distribution for immigrant species, in comparison, will tend to be left-skewed, spanning a range of younger ages. On islands that are close to a source, all species are immigrants and the more abundant species are older on average i.e. they usually colonised earlier (Fig. 5D). On more isolated islands, anagenetic species tend to be older than immigrant species and age correlates positively with abundance (Fig. 5E). The reason for this is simply that under ecological drift population increase is a slow process. Cladogenetic species have shorter ages because here "age" is the number of generations since the last split that left surviving descendants in the phylogeny for that species. The relationship between age and abundance for cladogenetic species is hump-shaped, with species of intermediate abundances generally being older (Fig. 5F). This is because the most abundant species are the ones most likely to give rise to sister species, which will then cause an abundant and otherwise ancient species to be regarded as being "young". However, if a sister species later goes extinct, the population "age" instantly reverts to being much older. One could argue that this scenario highlights a flaw in the way that species age is commonly calculated. In an alternative definition of age, each speciation event is not viewed as the splitting of one species into two, but the divergence of a subpopulation from its parent species. The age of the new species would be the date of divergence, but the age of the parent species would remain the earlier date that it broke away from its own parent species (Roy & Goldberg 2007). We also plot the ages of our cladogenetic species according to this definition, reinstating the correlation between age and abundance (Fig. 5F). The definition of age based on time to most recent common ancestor is, however, all that can realistically be measured empirically using current molecular phylogenetic approaches.

Future directions

We have compiled a new worldwide dataset of avian species on archipelagoes and presented the most parsimonious model that could credibly match these data and the observations of a variety of other existing empirical studies. The model is neutral in the sense that individual's probabilities of birth and death are independent of species identity, though individuals belonging to immigrant species do have an elevated chance of speciation because of the possibility for anagenesis that is not open to already endemic species. We are presented with a challenge relating our simulation model to the real world in that biologically realistic values for the duration of speciation $\boldsymbol{\tau}$ are not consistent with all speciation arising from neutral genetic processes (Gavrilets 2004). Therefore, by taking realistic values of $\boldsymbol{\tau}$, we implicitly include some, but not all, of the consequences of selection at the genetics level, whilst recognizing that speciation via natural selection departs from a strictly neutral model (Leibold & McPeek 2006). As our model does not include niches, it should be regarded either as a null model or as setting the foundations for a unified model for island biogeography to which additional complexity can be added (Bell 2001).

One area where there is potential for our model to provide a useful null is community phylogenetics. Recent studies have reported a tendency for island mammals to be phylogenetically overdispersed (Cooper *et al.* 2008), for the Caribbean anole diversification to slow through time on islands (Rabosky & Glor 2010) and for the per lineage diversification of a variety of taxa to be faster on young islands as compared with old islands (Gillespie 2004; Givnish *et al.* 2009). In all three cases competition and a role for the niche have been implicated as explanations, but it remains to be seen whether such patterns depart from a null expectation with no competition. Certainly, a tendency for the per lineage net rate of diversification to be faster on young islands will arise under a non-equilibrium version of our model because net diversification rates will be higher for two reasons. The island-wide extinction rate will be lower on young islands because of their low species diversity, a corollary of which is greater abundance of each species. Another consequence of low species diversity and large population sizes is that the per lineage speciation rate will also be inflated, even though the island-wide speciation initiation rate is constant.

While the assumptions of neutral theory have been criticized, we argue that a focus on dispersal and speciation as the two most important processes governing diversity on islands is likely to be less contentious. There are a variety of ways in which our model could be extended to explore the effects of introducing greater island biogeography realism. For instance, islands are often located in archipelagoes, and this could be incorporated by modeling each island as a separate patch with a matrix of immigration probabilities between patches. Larger islands might also be modeled as a collection of closely linked smaller islands (or habitat patches). Similarly departures from neutrality in the model could be explored, such as the incorporation of rare species advantage. This could be implemented with a "symmetric model" where species are interchangeable and have no specific traits, yet individuals can have differing birth and death rates depending on the density of conspecifics and heterospecifics. A study of the model's predictions outside of equilibrium also would be valuable, enabling investigations into the effect of island age (Stuessy 2007; Whittaker *et al.* 2008) and disturbance. We have experimented with two different functions for the immigration parameter m: proportional to area or coastline distance, but further possibilities could be considered.

Summary

MacArthur and Wilson (1967: page 5-6) wrote “*A main goal of this book is to identify those kinds of data needed for a further development of population theory and, ultimately, the full explanation of distribution itself*”. We have similar aims and hope that the existence of a quantitative model for species abundances on islands will inspire the collection of new data to test its predictions. Our prediction that endemic species should have relatively large population sizes may prove valuable, as conflicting observations might indicate human interference or be evidence for additional biological factors, such as the role of specialist enemies restricting the abundance of old endemics as postulated under the taxon cycle (Ricklefs & Cox 1972). We show that a threshold island area for *in situ* speciation can be explained with a fixed per capita rate of speciation without needing to directly invoke elevated numbers of barriers promoting vicariance or niches promoting ecological speciation. The model predicts that the gradient of the species-area curve in log-log space will be greater for endemics as compared with when all species, including immigrants, are counted. Anagenetic species are predicted to be in their highest numbers at intermediate distances from the mainland. Our model and the avian dataset have unified several existing models and ideas (Heaney 2000; Hubbell 2001; Whittaker *et al.* 2008). We show that observed patterns of species richness and endemicity on islands can be understood as an emergent behavior of a simple model of immigration and speciation. In doing so, we offer a quantitative foundation for future island biogeography research.

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Figure legends

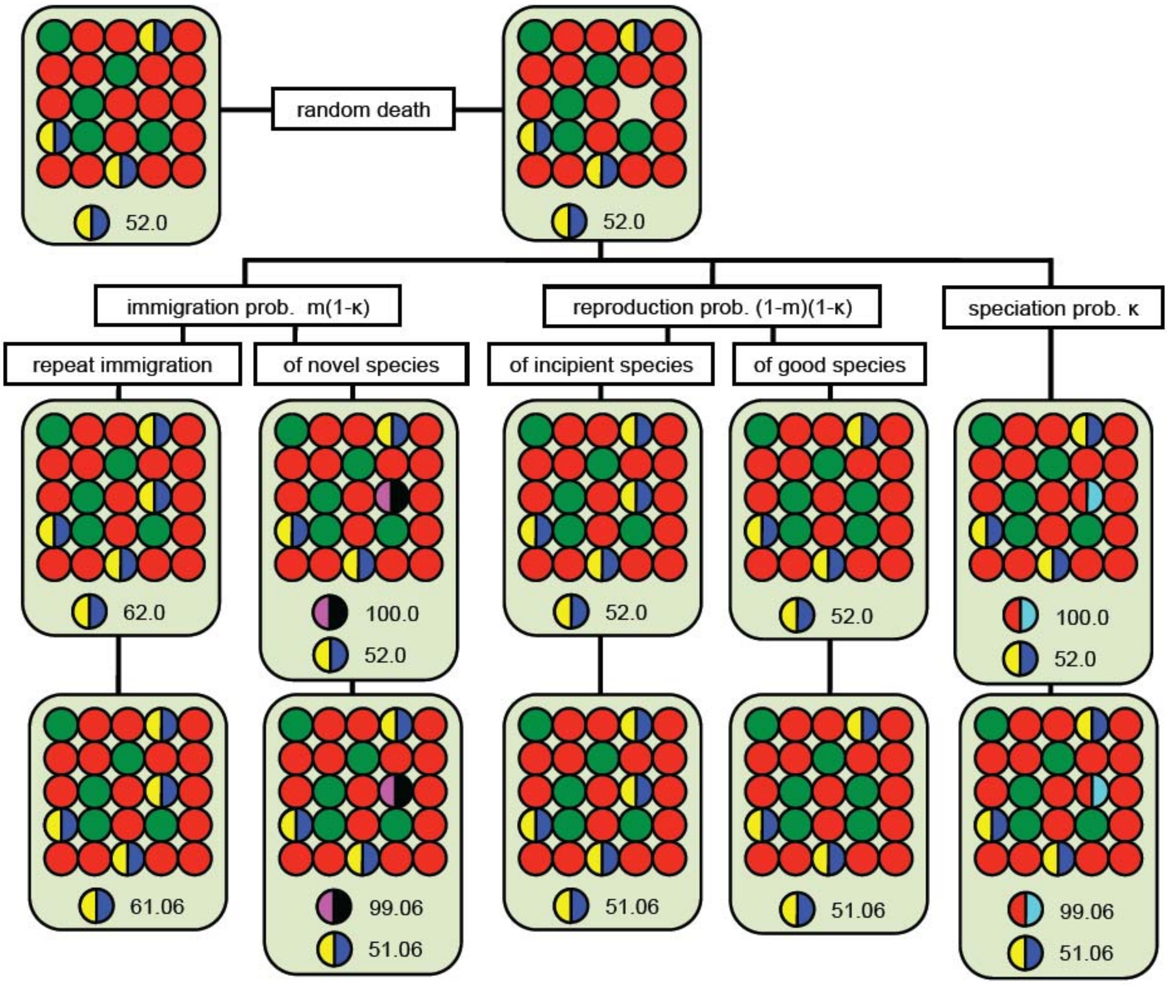

Figure 1.

Schematic representation of the individual-based model used in this study. Variants are shown in two colors rather than one - the first color represents its parent species and the second color represents the species it is in the process of becoming. Good species are shown in solid colors. There are 25 individuals and the illustrated step represents 1 death and 1 birth: that is 1/25 = 0.04 of a generation. Transition time τ = 100 and gene flow effect G = 10 in this example κ is the speciation initiation rate. The numbers at the bottom of each section of the schematic represent the remaining waiting times to speciation (in generations) for each of the variant species indicated.

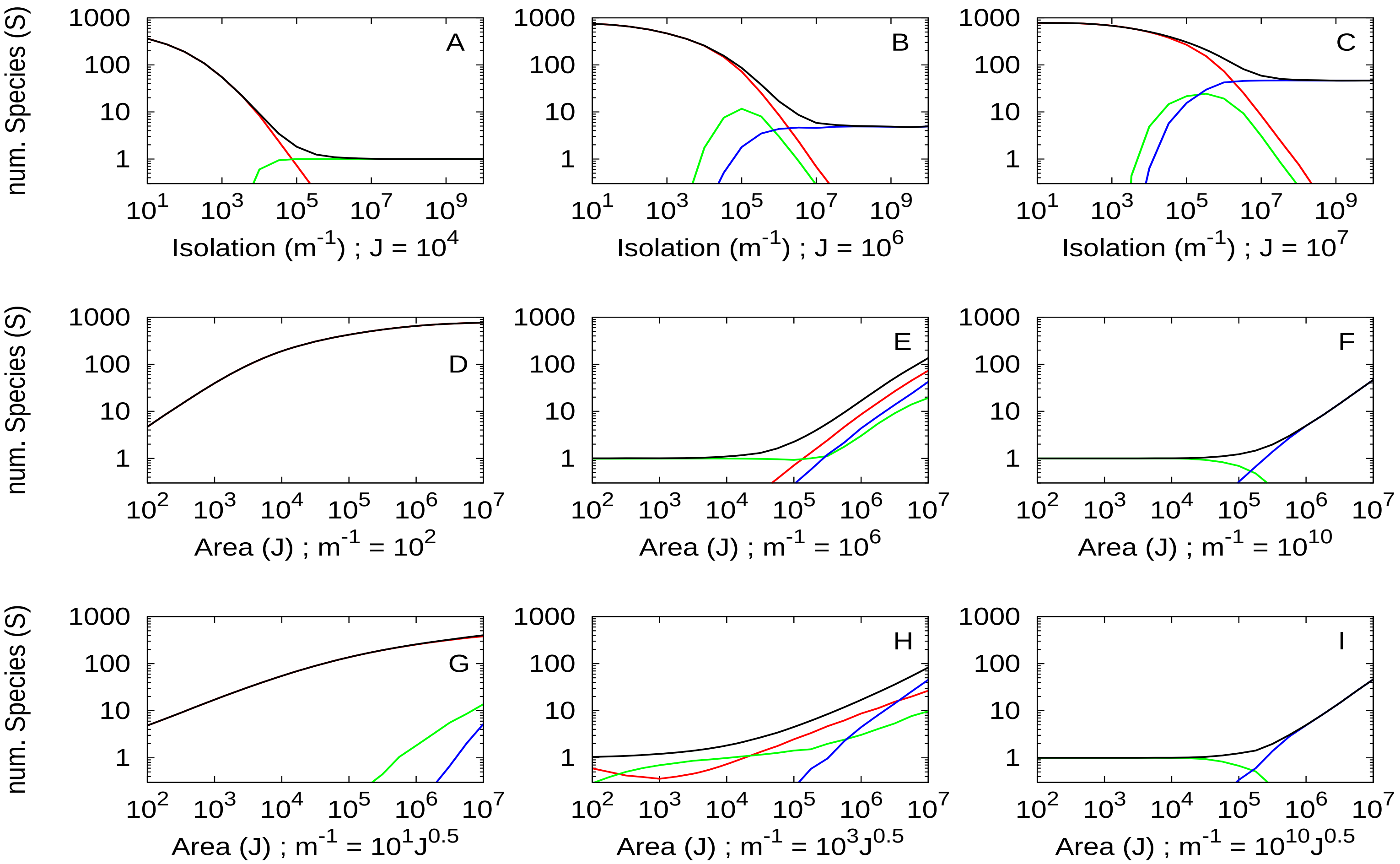

Figure 2.

Species-isolation (A-C) and species-area (D-I) curves for cladogenesis initiation rate $\kappa = 10^{-6}$, duration of speciation $\tau = 10^4$ and gene flow effect $G = 10$. Immigration rate is proportional to area in panels D - F and proportional to coastline in panels G -I. The colored lines correspond to the richness of different classes of species: red show immigrants, green shows anagenetics, blue shows cladogenetics and black shows the total species richness. Results are the means over at least 1024 repeat simulations of the log of the richness + 1.

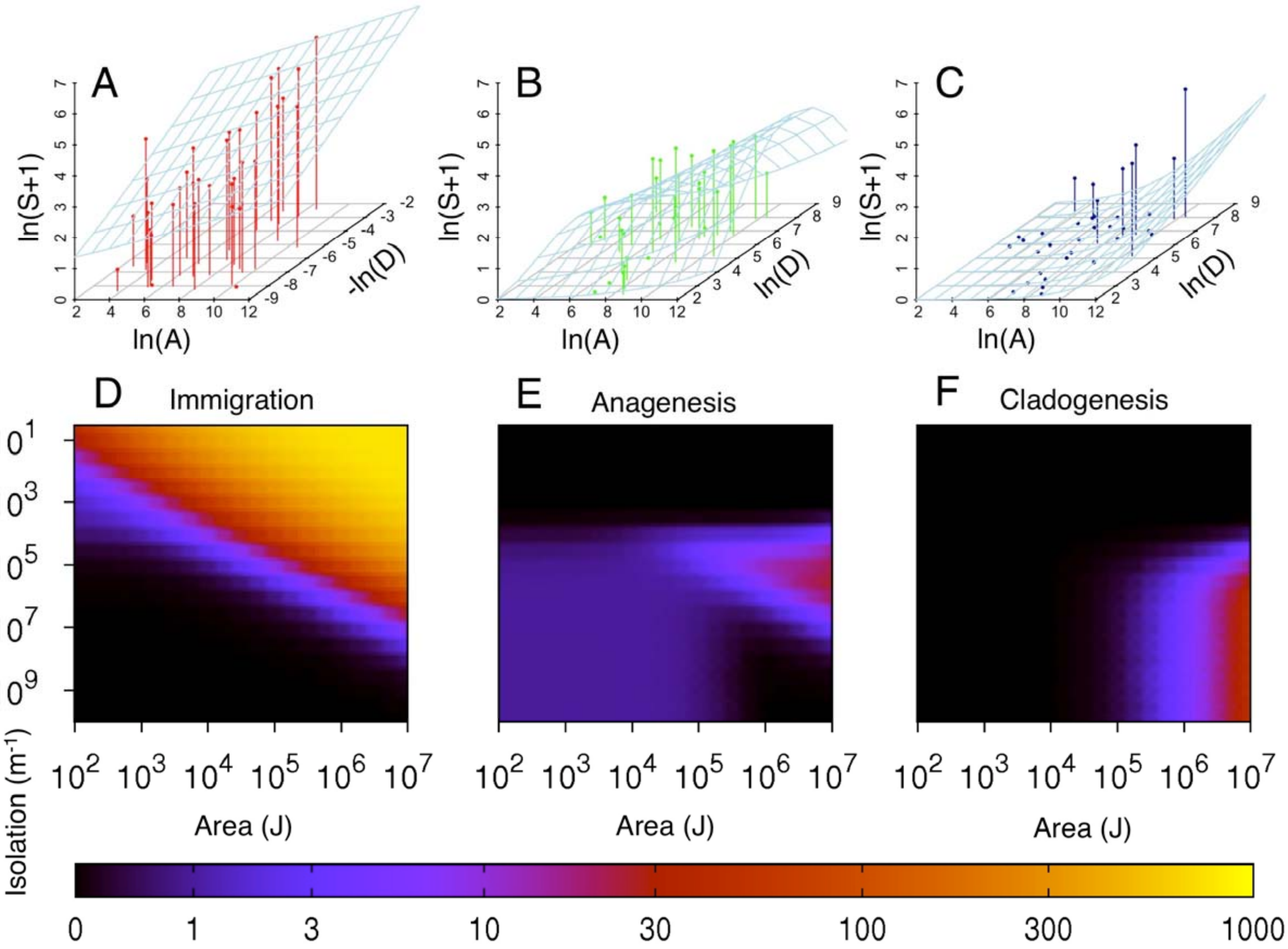
A
B
C
ln(S+1)
ln(A)
-ln(D)
ln(D)
D
Immigration
E
Anagenesis
F
Cladogenesis
Isolation (m-1)
Area (J)
0
1
3
10
30
100
300
1000

Figure 3.

Avian species richness in relation to archipelago area and isolation, for A. immigrant, B. anagenetic and C. cladogenetic species. Together with the equivalent model predictions in panels D-F. In plot A the sign of the isolation axis has been changed to make the relationship more visible. The parameter and model fit estimates on a log scale were: A. Immigrant species richness = Intercept 4.77 [±0.65, ***] + Area 0.18 [± 0.07, *] + Isolation -0.45 [± 0.06, ***]; B. Anagenetic species richness = Intercept -8.82 [± 2.96, **] + Area 0.32 [± 0.07, ***] + Isolation 2.88 [± 0.97, **] + Isolation^2 -0.24 [± 0.08, **]; C. Cladogenetic species = Intercept -11.59 [± 3.07, ***] + Area 1.10 [± 0.28, ***] + Isolation 0.50 [± 0.24*]. In all cases $n = 35$ archipelagoes. *, ** and *** correspond to $p < 0.05$, 0.01, and 0.001. Simulation parameters were as Fig. 2, but predictions are robust to other choices.

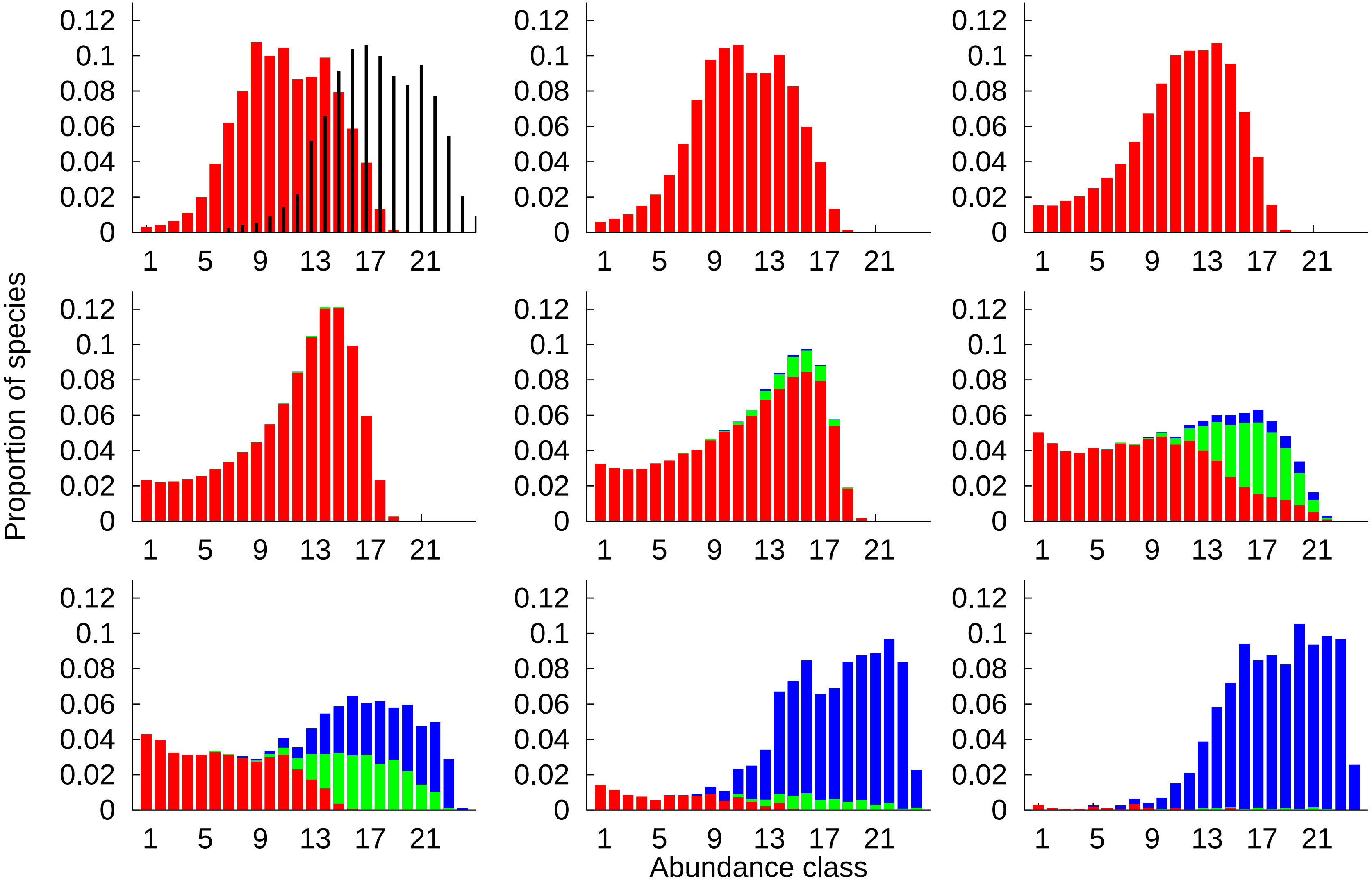
Proportion of species
0.12
0.1
0.08
0.06
0.04
0.02
0
1
5
9
13
17
21
Abundance class

Figure 4.

Species abundance classes as a function of isolation. The nth bar shows species with abundances greater than or equal to n and less than 2n. Black bars show the abundance distribution on the mainland, colored bars show how that abundance class is broken down into immigrant (red), anagenetic (green), and cladogenetic (blue) species. All graphs were for area $J = 10^7$, cladogenesis initiation rate $\kappa = 10^{-7}$, duration of speciation $\tau = 10^4$ and gene flow effect $G = 10$. The immigration parameter was given by $m = 10^{-1}$ in the top left panel, and decreased by a factor of 10 in each subsequent panel from left to right, then top to bottom so that in the bottom right panel $m = 10^{-9}$.

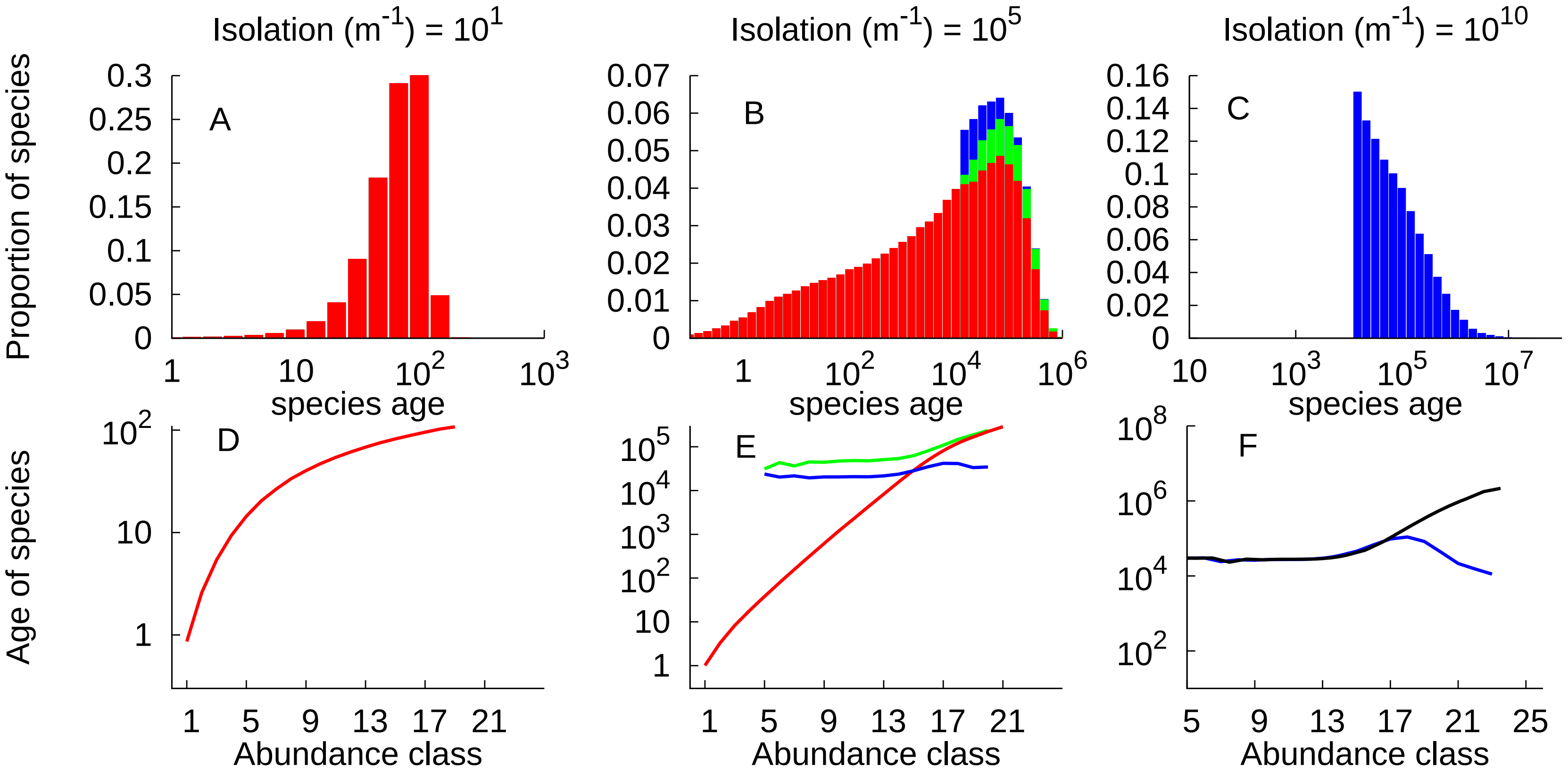

Figure 5.

The distribution of species ages (A-C) and the mean log age as a function of species abundance (D-F). Colors correspond to immigrants (red), anagenetic (green) and cladogenetic (blue). In panel F the black line shows the ages of cladogenetic species defined as the date of divergence from a parent species, all other ages are based on the divergence date from the phylogenetic tree, for immigrant species the time since immigration is taken. All graphs were for area $J = 10^7$, cladogenesis initiation rate $\kappa = 10^{-6}$, duration of speciation $\tau = 10^4$ and gene flow effect $G = 10$.