

A unified model of species immigration, extinction and abundance on islands

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ABSTRACT

Aim MacArthur and Wilson's theory of island biogeography was revolutionary, and also inspired the more recent unified neutral theory of biodiversity and biogeography. The unified neutral theory has the potential to make predictions about island biogeography that are not well studied. Here we aim to unify the two theories by using an ecological neutral model to study immigration and extinction rates on islands – the cornerstone of MacArthur and Wilson's theory.

Methods We conduct simulations of a spatially implicit neutral model and measure species abundances, immigration rates and extinction rates. We study the behaviour of the model at dynamic equilibrium and on approach to dynamic equilibrium both from volcanic origin (low initial diversity) and from land bridge origin (high initial diversity). We extend the model to study the effects of clustered immigration and to explicitly account for the distinction between immigration and colonization.

Results Our model, in accord with the simplest version of MacArthur and Wilson's theory, predicts linear immigration and extinction rates as functions of species richness at dynamic equilibrium. In contrast, the approach to dynamic equilibrium produces rich and unexpected behaviour where immigration and extinction rates are non-monotonic functions of species richness, at odds with other theory. Once examined, however, this behaviour makes biological sense and results from the influence of the species abundance distribution over immigration and extinction rates. The turnover predicted by our first model appears high, but can be lowered to realistic levels with an alternative model of clustered immigration or by accounting for the difference between the immigration of a new species and its true colonization of the island.

Main conclusions MacArthur and Wilson's theory of island biogeography and ecological neutral theory are different, but there are strong similarities in their assumptions and predictions that should not be overlooked when evaluating them. Our results highlight the importance of species abundances as indicators of immigration and extinction rates; species richness alone is insufficient. In particular, extinction rate and species abundances are unavoidably linked, as rarity usually precedes extinction.

Keywords

Biodiversity, colonization, dynamic equilibrium, immigration, island biogeography, land bridge island, neutral theory, volcanic island.

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INTRODUCTION

MacArthur & Wilson's (1963, 1967) equilibrium theory of island biogeography (ETIB) caused a revolution in the field of island biogeography and continues to inspire a tremen-

dous interest (see chapters in Losos & Ricklefs, 2010). The central concept of the ETIB was a dynamic equilibrium in species richness where immigration of new species was balanced by local extinction. Under the ETIB, both immigration and extinction rates on islands are functions of island species

richness, assumed linear in the simplest case, but allowed to be concave in other versions. The ETIB is perhaps best known for its iconic diagrams showing immigration and extinction rates against species richness, with the species richness at dynamic equilibrium (hereafter just equilibrium) being given where these two lines cross. Many of the predictions and assumptions of the ETIB were verified empirically, first by Simberloff & Wilson (1969) and later by others, reviewed by Schoener (2010). The ETIB does not have universal support from empirical data; for example, Bush & Whittaker (1991) argue that it would take so long for volcanic islands to reach equilibrium that the frequency of volcanic disruptions will prevent the system from ever reaching this state. Consequently, there is a growing interest in the disequilibrium behaviour of volcanic islands (Whittaker *et al.*, 2008) and a clear need for more quantitative theory for islands that are not at equilibrium (Heaney, 2000).

More recently, a spatially implicit individual-based neutral model was introduced inspired partly by the ETIB. This model is the best known of a number of models within 'The unified neutral theory of biodiversity and biogeography' (Hubbell, 2001) and it shares key features with the ETIB. In particular, it features a 'local community' (interpretable as an island) where local extinction is in equilibrium with immigration from the 'metacommunity' (interpretable as the mainland). Like the ETIB, the neutral spatially implicit model can predict species richness as island size and isolation vary (we refer to the neutral spatially implicit model as the NSIM from here on). Whilst it has often been referred to as UNTB in the past (after the unified neutral theory of biodiversity and biogeography), this terminology confuses the general concept of neutral theory with one particular neutral model; many other neutral models are also available (reviewed in Rosindell *et al.*, 2011). The applicability of ecological neutral theory in a non-neutral world has been debated, but it is not the purpose of this work to repeat the existing commentary on this issue (Rosindell *et al.*, 2011, 2012). Our perspective is that a model need not be completely realistic in order to be worthwhile and useful (Wennekes *et al.*, 2012).

The key difference between MacArthur and Wilson's ETIB and the NSIM is that the latter operates at the level of individual organisms. Individuals – not species – immigrate onto the island under the NSIM, although we note that Azovsky (1988) studied equilibrium density of individual ciliates on sand islands in the context of the ETIB. One major advantage of individual-based models is the possibility of predicting patterns of species abundances rather than just presence and absence. The potential benefits of adopting an individual-based neutral model, such as the NSIM, as a new standard for island biogeography have been highlighted from the start (Hubbell, 2001) and lately reiterated (Hubbell, 2010; Rosindell & Phillimore, 2011). For example, an extension of the NSIM incorporating a more realistic speciation process was recently successfully used to predict patterns of endemic and immigrant species and their abundances on islands

(Rosindell & Phillimore, 2011). In general, however, the NSIM has rarely been applied to investigate key concepts in island biogeography. Immigration and extinction rates as a function of species richness formed a cornerstone of the ETIB. It is therefore pivotal to the integration of the ETIB with neutral theory that the NSIM predictions for these rates are understood. Previous work considered this, and predicted concave immigration and extinction curves arising from the NSIM (Hubbell, 2010), consistent with the more advanced (and often described as non-neutral) version of the ETIB. The earlier work was, however, restricted to extremely high immigration rates and did not make the critical distinction between equilibrium and non-equilibrium cases.

Here we show the immigration and extinction rates for the NSIM at equilibrium and on approach to equilibrium separately, for new islands that have been created by the removal of a land bridge (high initial diversity), or by volcanic activity (low initial diversity), and for a wide range of immigration rates. We find that the fluctuations around the equilibrium in the NSIM are in fact apparently linear and strikingly similar to the simplest (often described as neutral) version of MacArthur and Wilson's theory. In contrast, on approach to equilibrium, the individual-based nature of the NSIM leads to rich and complex behaviour with the immigration and extinction rates often following non-monotonic functions of species richness completely unlike those assumed by the ETIB. We find that rates of species turnover per generation predicted by the NSIM are probably higher than would be thought to be realistic in actual data, a point not commented on in earlier work (Hubbell, 2010). We were able to resolve this problem with more advanced variations of the model that involve clustered immigration or ways to account for the distinction between immigration and colonization.

METHODS

The basic model

Our simulations are based on the NSIM and variations of it. The code was written in C++ and is provided as supporting information in Appendix S1. In our simulations, there is an island and a mainland. On the island, in every time step, an individual organism dies leaving a habitat gap. The gap is then immediately filled with the birth of another individual (the zero sum assumption; Hubbell, 2001). With probability $(1 - m)$ this newborn is an offspring from a randomly chosen parent individual within the island. Each individual in the island is equally likely to be chosen as the parent so within-island spatial structure is not explicitly modelled. Alternatively, with probability, m , the newborn is the offspring of a randomly chosen individual in the mainland (Fig. 1). The species identity of the newborn will always be the same as the species identity of its parent. We define a single generation in this model as the mean lifetime of an individual organism. This is a study of immigration and

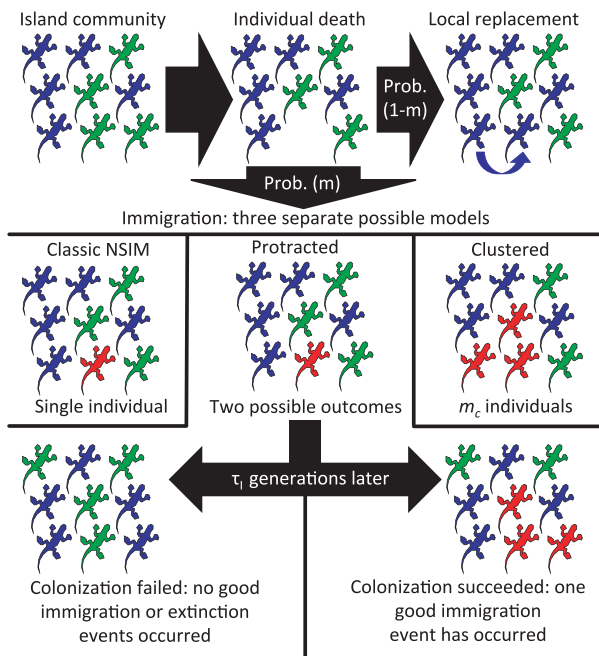


Figure 1 A schematic showing the basic immigration model of the neutral spatially implicit model (NSIM) compared to our clustered immigration model and protracted immigration model. Abbreviations: m , immigration rate; m_c , number of conspecific immigrants in clustered immigration; τ_i , number of generations required for immigrant populations to become colonized in protracted immigration.

extinction (not of speciation) and thus, in common with Hubbell's best-known model, there is no speciation on the island. For a study of within-island speciation based on neutral theory we refer readers to Rosindell & Phillimore (2011). Note that there is no explicit treatment of sexual reproduction in most ecological neutral models. Perhaps the best way to interpret this is that only females are considered, but the abundance of females would be strongly correlated with the total abundance of the species. The immigration probabilities of an individual (female) would then implicitly encompass the additional barriers of colonization (e.g. arriving pregnant, arriving with a male, or finding a male already present).

The mainland

In the original NSIM, the mainland (metacommunity) abundance distribution, from which immigrating individuals are drawn, was assumed to be a fixed log-series distribution and the immigration probabilities for each species were interpreted as being given by their relative abundance on the mainland. In our implementation, we have a similar pool of species on the mainland, each of which has a fixed abundance, but we relax the requirement for this to be a log-series – it could take any form. In a purely neutral implementation, these probabilities would differ only because species have different abundances on the mainland. In reality, however, there will be other differences between species

that influence their probability of immigration onto the island. It is important to recognize that the distribution of immigration probabilities could be reinterpreted in a non-neutral way without changing the model itself, or its predictions. For example, the immigration probabilities could represent the combined effects of both mainland abundance and long-distance dispersal ability for each species. For our simulations, we use two different distributions of immigration probabilities of species:

1. A uniform distribution consisting of a pool of 1000 species, each with an equal chance of having an individual immigrate to the island.
2. A 'difference log-series' distribution (Rosindell *et al.*, 2010), which after sampling appears similar to a log-series, but which unsampled has fewer rare species.

If a trade-off exists between immigration probability and mainland abundance (Levine & Rees, 2002; Kneitel & Chase, 2004) then more abundant species on the mainland would be less likely to immigrate (per capita); however, there would be more individuals of that species with the potential of immigration, so net immigration probabilities would approach a uniform distribution. A log-series distribution of abundances would arise on the mainland under a non-spatial neutral model where dead individuals are, with probability $(1 - \nu)$, replaced by the offspring of randomly chosen individuals and, with probability ν , are replaced with the founding individual of a new species. The difference log-series distribution of mainland abundances comes from a similar non-spatial neutral model but where speciation is a gradual process (protracted speciation), rather than an instantaneous event (point mutation speciation) (Rosindell *et al.*, 2010). The hump shape of the difference log-series when plotted on a logarithmic scale (in 'octaves') is qualitatively similar to Preston's log-normal distribution (Preston, 1948). The difference log-series is, however, more closely allied to the log-series (Fisher *et al.*, 1943) in terms of its mathematics and its quantitative predictions for the common species tail of the distribution. The difference log-series is thus an improvement on the log-series distribution that incorporates similarities with the log-normal and other distributions. In the present work, we created our difference log-series using a speciation initialization rate of $\mu = 10^{-7}$, a mainland carrying capacity of $J_M = 10^9$ individuals and duration of speciation of $\tau = 10^4$ generations (Rosindell *et al.*, 2010). We do not, however, expect the precise details to affect our main conclusions.

Approaches to equilibrium

We studied two distinct approaches to equilibrium: volcanic origin islands and land bridge origin islands. The land bridge origin scenario corresponds to a case where part of the mainland becomes an isolated island, for example as a result of sea level rise. To simulate this we used the initial condition of an island containing a random sample of individuals from the mainland species abundance distribution. Such an

island is then supersaturated: it would naturally have an initial richness higher than that expected at its new equilibrium as a more isolated habitat. In contrast, the volcanic origin corresponds to the case where a fresh island appears already isolated from the mainland. Neutral theory typically only applies to a particular guild; a single neutral model cannot capture the interaction between guilds (Hubbell, 2001). Consequently, the time a volcanic island spends unpopulated for the guild of interest is outside the scope of the model. The most appropriate initial condition for an island of volcanic origin is thus a single population on the island corresponding to a species richness of one, which is clearly lower than the richness expected at equilibrium after other species colonized. Within the chosen guild, the species chosen to initially populate a new volcanic island was the mainland species with the highest probability of immigration. In this context of a single guild neutral model, alternative choices for the first colonizing species would be of little consequence to the approach to equilibrium because the arrival and local extinction of later colonizers will dominate the dynamics and be largely independent of which species from that guild was the first to colonize. In the context of a real volcanic island undergoing succession with different guilds arriving in an ordered fashion, the first colonizer would indeed be important, but such a model is outside the scope of this work.

Simulation methods

We keep track of the abundances of all species at all times, and record the species richness of the system whenever a species immigrates or goes extinct. To obtain rates of immigration and local extinction that are not specific to a particular richness, we would divide the total number of immigration (or extinction) events by the total time (in generations) for which we were measuring. To obtain rates as a function of species richness we must divide the number of immigration (or extinction) events occurring *at that species richness* by the total time that the system spent *at that species richness*. If the system did not fluctuate to a given species richness very often, then reliable rates could not be calculated and we excluded them.

To obtain immigration and extinction rates from the model in approach to equilibrium, we took readings continuously from initialization until the system reached equilibrium. We then took further readings to determine the behaviour of the system at equilibrium, where it still fluctuates a little to either side of the equilibrium richness value. We define the system as having reached equilibrium when the initial conditions are no longer influencing its present state. Another commonly used definition of equilibrium is that it occurs when immigration and extinction rates are equal (on average); however, this is distinct from (and weaker than) our definition. If the initial condition no longer influences the state of the system (the system is at equilibrium by our definition), then initial conditions of extremely high diversity or extremely low diversity would be equally

likely to lead to the present state of the system and that must mean currently balanced immigration and extinction rates. When one considers the abundances of species, immigration and extinction rates might be balanced whilst the system has not yet really reached equilibrium; this could occur where the total species richness has reached a steady state, but not the species abundance distribution.

According to our stronger definition of equilibrium suitable for individual-based models, equilibrium requires all individuals of the island to be descendants of those that have immigrated during the simulation so that no individuals are descendants of the individuals present in the initial conditions of the simulation. To determine when this occurs, we label every individual on the island with a Boolean flag set to 'true' at the start of the simulation. The flag attached to any given individual indicates whether it is a descendant of the individuals initially present forming the initial conditions (true) or not, in which case it is a descendant of some individual that immigrated during the simulation (false). With every reproduction event within the island the state of the Boolean flag as well as the species identity gets passed from parent to offspring. Immigration events from the mainland bring in new individuals, so have a 'false' flag. The system has reached equilibrium once all currently living individuals have a Boolean flag value of false. After reaching equilibrium (from either land bridge or volcanic origin) we reset all the flags to true and continue running the system until they have once again reverted to false – this gives us results at equilibrium with an approximately equal number of readings to those taken outside equilibrium. Because the simulation results were stochastic, we conducted as many repeat simulations as possible with the constraint that no more than 8 days of computer time could be used for each parameter set. This protocol enabled us to get accurate pictures of the immigration and extinction curves from the models without spending a disproportionately large amount of resources on any particular scenario. There were between 348 and 725,450 complete simulations for each set of parameters; the median number of simulations was 34,200.

Immigration models

We experimented with alternative and more realistic models of immigration than those defined in the original NSIM. To see why this may be needed, imagine the case where a breeding pair of birds are blown off course by freak winds and settle on an island where they are non-native and the only ones of their kind. If a few days later they go elsewhere (or die), this is not really an immigration event followed by a local extinction – although strictly speaking one should count it (MacArthur & Wilson, 1967). In practice, a 'good immigration event' is the colonization of a species: its survival and establishment on the island as a viable population. To resolve this issue in a variation of the NSIM, we experiment with 'protracted immigration' (after 'protracted speciation'; Rosindell *et al.*, 2010) where an immigration event

(and the corresponding local extinction that occurs later) only counts towards the rates if the species survives on the island for a certain predefined number of generations given by τ_I (Fig. 1). The immigration date is the date where the immigrant population became a good immigrant species (fully colonized rather than merely present). By increasing τ_I one can see the effects of increasingly stringent definitions of colonization in an otherwise identical model – a refinement that makes good biological sense. We do not expect the difference between colonization and immigration to have been as relevant in the original ETIB because this original model did not consider the commonness or rarity of a species, and thus recent immigrants would not be especially vulnerable, as they are in the NSIM.

A further alternative ‘clustered immigration’ model allows species to arrive on the island as small groups (Fig. 1). This could be interpreted as flocks of birds arriving, clustered seed dispersal or a way to model implicitly a non-neutral competitive advantage that new immigrants might initially enjoy due to the enemy release hypothesis (Keane & Crawley, 2002). There is a variable m_c that controls the number of individuals associated with each immigration event. The immigration rate of individuals (m) is still respected so that instead of having one immigrant arrive with probability m per death, we have m_c conspecific immigrants arrive, but

with the smaller probability of m/m_c . In order to maintain the zero sum assumption, rare clustered immigration events are accompanied by m_c deaths of individuals on the island to make space for the m_c new immigrants. This may be implicitly interpreted as new immigrants outcompeting a number of natives due to selective advantage. These sudden deaths may seem unrealistic; however, if one accepts the premise of a carrying capacity for the number of individual organisms on the island in a particular guild, such deaths are inevitable. Modelling clustered immigration any other way would involve relaxing the zero sum assumption, which is already known to have little effect on the predictions of similar neutral models (Etienne *et al.*, 2007).

RESULTS

A typical set of parameters reveals very different behaviours for equilibrium, volcanic origin and land bridge origin islands (Fig. 2). For a system that has reached an equilibrium, its fluctuations about this equilibrium reveal close to linear relationships between species richness and rates of immigration or extinction – in perfect accord with the simplest version of the ETIB (Fig. 2b). We note that our model does not generally move far from its equilibrium state when at equilibrium. The models’ dynamics are also slower at

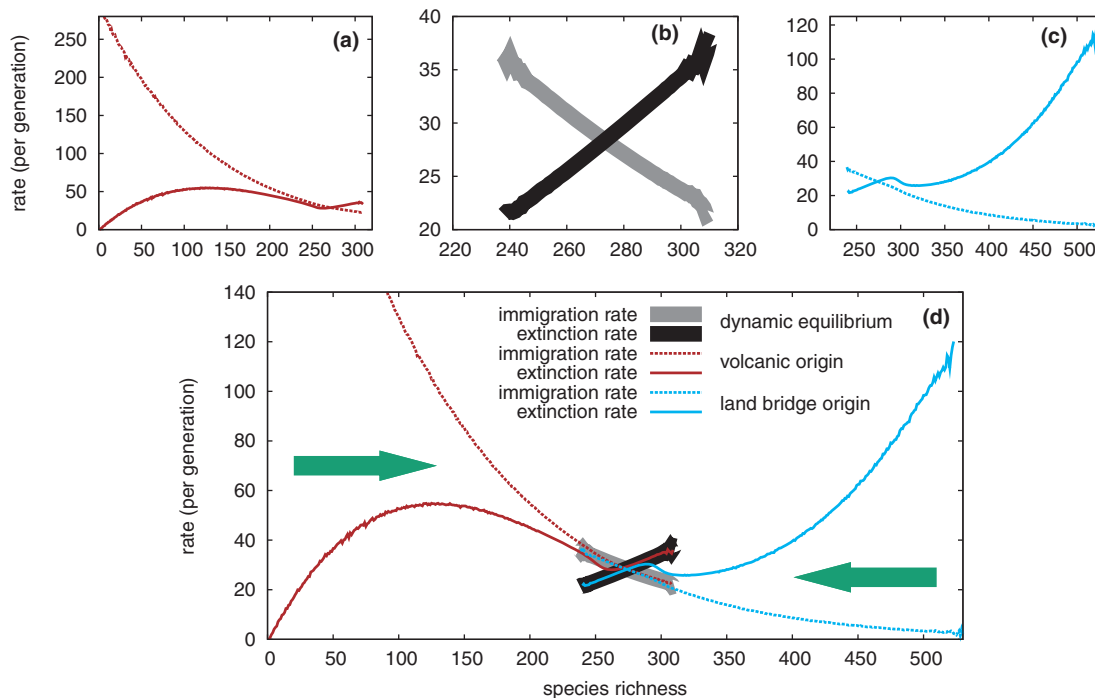


Figure 2 Immigration rate and extinction rate curves for (a) islands of volcanic origin, (b) islands at dynamic equilibrium (where the island’s origin no longer influences its present state – see main text), and (c) islands of land bridge origin. Panel (d) presents the data from all panels (a–c) together to enable them to be compared and contrasted. The green arrows show the progression of species richness towards equilibrium from both high diversity (land bridge origin) and low diversity (volcanic origin) initial conditions. All these data were for a difference log-series mainland immigration probability distribution, immigration rate $m = 0.03$ and island size $J = 10,000$ individuals. In the model, individuals (and not species) are the entities arriving on an island; however, in these graphs we count the arrival of new species, which occurs when an individual arrives of a species not already present on the island.

equilibrium compared with the period of approach to equilibrium. This may be one testable difference between our model and that of the original ETIB.

The volcanic origin case (Fig. 2a) has an initial species richness of one, a zero extinction rate and a high immigration rate so that species richness increases rapidly through time. The per species extinction rate increases from zero as species richness increases, but then peaks at an intermediate species richness and starts to decrease, eventually becoming closely correlated with the immigration rate. The immigration rate remains higher than the extinction rate and thus species richness is gradually increasing. As the system settles down into equilibrium there is a sudden turn in the extinction rate curve before it converges to the linear behaviour of equilibrium.

The approach to equilibrium from a land bridge scenario (Fig. 2c) involves a per species extinction rate that is curved and decreases with decreasing species richness. There is a similar turn in the extinction curve as it gets close to equilibrium. The extinction rate curves for the land bridge origin case do change significantly for a mainland containing species with equal abundances: the extinction curve for high diversity is zero (Fig. 3i–l) and apparently increases with decreasing diversity until it peaks and begins to fall.

The immigration curves depend less strongly on whether or not the system is at equilibrium and instead depend on the distribution of immigration probabilities across species. In all cases, the immigration of individuals happens at a constant rate regardless of species richness; however, repeat immigration of a species already present does not constitute immigration, only a change in population size. The immigration curves are thus influenced by the richness on the island. If all mainland species have equal abundances (Fig. 3i–l) then the immigration curve is a straight line. When mainland species have different abundances given by a difference log-series the immigration curve decelerates with increasing species richness (Figs 2 & 3a–h) in agreement with the apparently ‘non-neutral’ version of the ETIB that has concave immigration curves (MacArthur & Wilson, 1963, 1967).

Exploring the phase space of the model with different immigration rates and island sizes reveals no important change to the qualitative patterns for immigration and extinction curves (Fig. 3). Of course the species richness and turnover rates at equilibrium are still affected by these parameters. For example, if immigration rate is very small, the system’s approach to its equilibrium of low diversity, from low initial diversity (volcanic origin), is not meaningful because the system does not have far to travel to reach its

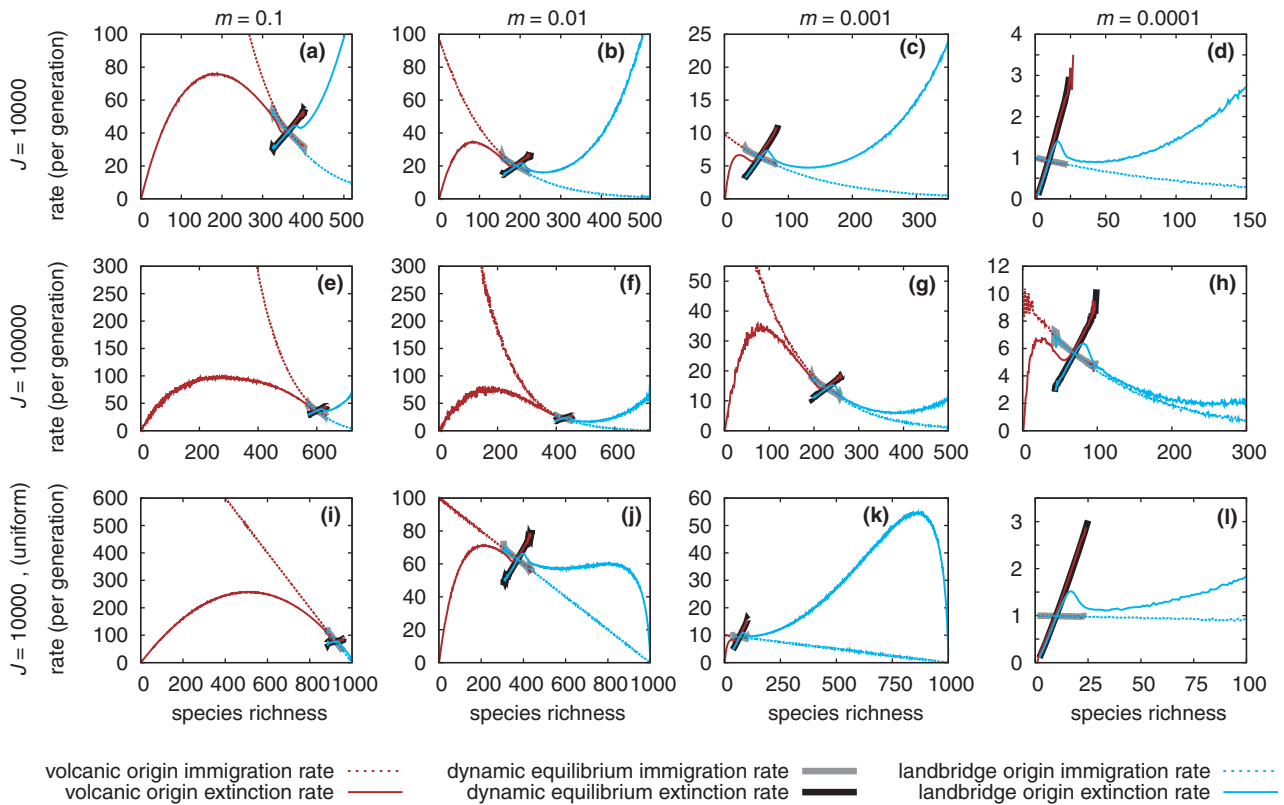


Figure 3 Each panel shows, for a different set of parameters, the immigration rate and extinction rate curves for volcanic origin, dynamic equilibrium and land bridge origin scenarios. Each column represents a different immigration rate (m). The first two rows represent local communities of different sizes (J individuals) receiving immigrants from a mainland with difference log-series distributed species abundances; the third row shows an island with fixed size receiving immigrants from a mainland where all species have equal abundances – the scenario that would produce two straight lines under the equilibrium theory of island biogeography.

equilibrium (Fig. 3d,l). A larger island can have high diversity even with small immigration rates and thus can have a meaningful approach to equilibrium from low diversity (Fig. 3h).

The effect of the exact species abundance distribution on immigration and extinction rates is shown in Fig. 4, where species abundance distributions were drawn for three different species richness values. In this example, at a low richness of 250, the volcanic origin extinction rate is much higher than that for equilibrium and land bridge origin cases of the same richness (Fig. 4a). The reason is now clearly identified: the species abundance distribution shows many more rare species and fewer common species in the volcanic origin case, compared with the other cases that agree almost perfectly with one another. Similarly at a high species richness of 300, the lower extinction rates for land bridge origin are revealed as being caused by there being fewer rare species (Fig. 4c). The exact richness values where these behaviours are seen will depend on the model's parameters, but like our other results, the patterns themselves are robust to changes in parameters (Fig. 3).

In the results presented thus far, immigration and extinction rates were probably too high to be considered realistic. Both protracted immigration and clustered immi-

gration offer good solutions to this problem (Figs 5 & 6). Protracted immigration results counted colonization events only when immigrant species survived on the island as a population for τ_i generations. More stringent requirements on what constitutes a colonization event (larger values of τ_i) reduced turnover dramatically. Furthermore, the behaviour of the immigration and extinction curves became more like the smooth arcs of MacArthur and Wilson's theory, although we note that the unusual dynamics as equilibrium is approached do not disappear entirely (Fig. 5). The immigration rate curve in the volcanic origin case increases from an initial value of zero because there is a delay between immigration and colonization; thus colonization rates take a short period to build up to their true level, by which time the species richness has increased. Under the clustered immigration model, where new species arrive with abundances greater than one, the species turnover is low and the curves are closest of all to what would be expected from MacArthur and Wilson's theory, with curved forms for the immigration rate and extinction rate as a function of species richness (Fig. 6). As with the results for protracted immigration (Fig. 5), there is still a sign of more complex behavior, with the curves not always being monotonic.

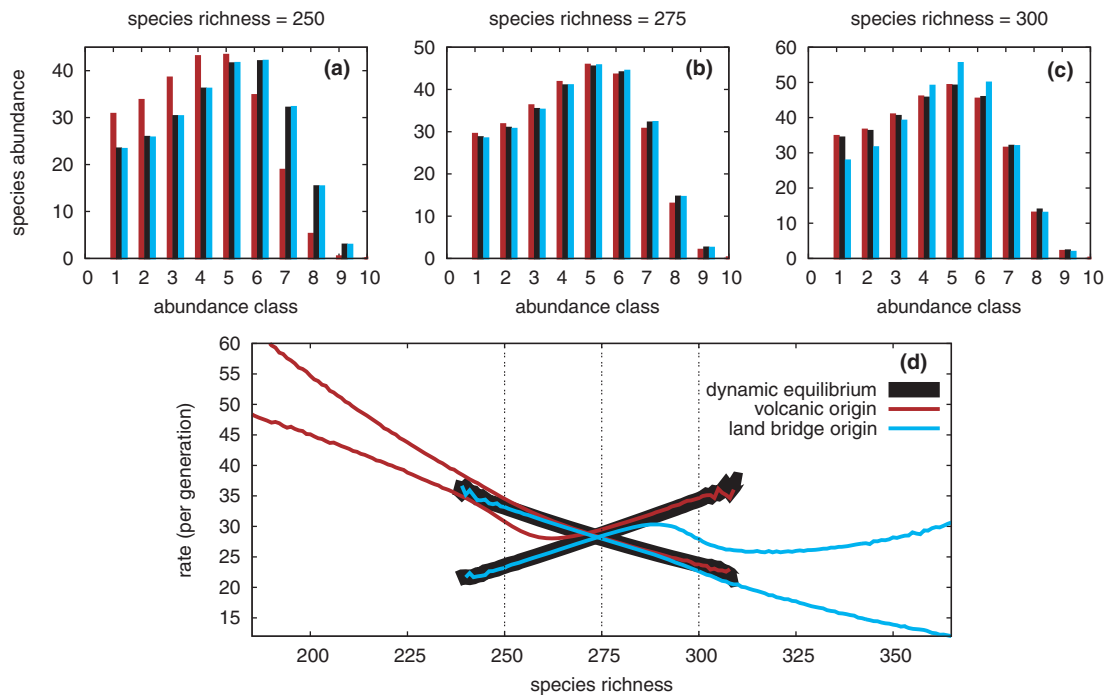


Figure 4 The link between species abundance distributions and the immigration and extinction rates. Panels (a)–(c) show the expected species abundance distributions for exactly these three species richnesses under the equilibrium, volcanic origin and land bridge origin cases separately. The species abundance distribution is presented as abundance classes with the first bar showing singleton species, the second bar showing those with abundance 2 or 3, and in general the n^{th} bar showing the number of species with abundance $\geq 2^n$ but strictly $< 2^{(n+1)}$. Panel (d) presents immigration rate and extinction rate curves for volcanic origin, dynamic equilibrium and land bridge origin scenarios using parameters immigration rate $m = 0.03$ and island size $J = 10,000$ individuals. Both axes are rescaled to expand on the section around the equilibrium and final stages of approach towards it. Immigration rate and extinction rate curves are not distinguished. The vertical black lines on this panel are at richnesses of 250, 275 and 300.

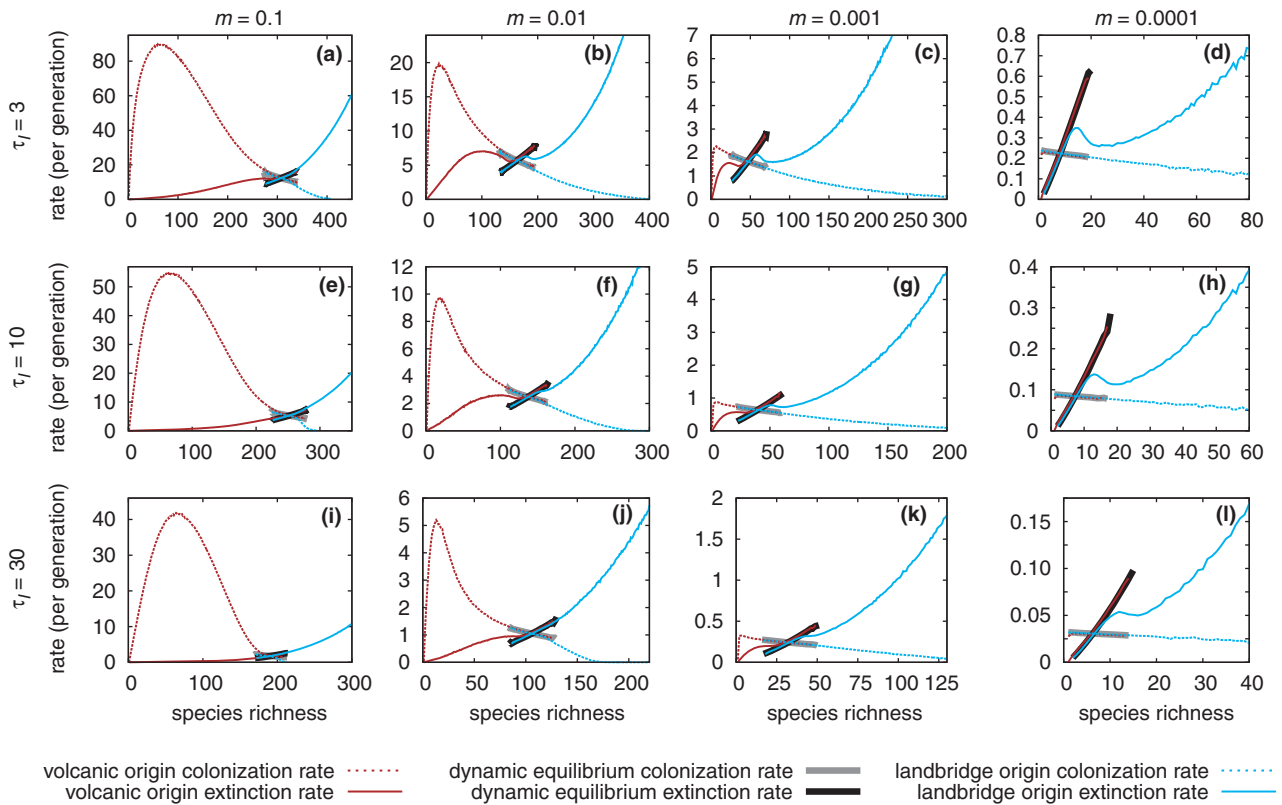


Figure 5 Protracted immigration results: each panel shows, for a different set of parameters, the immigration rate and extinction rate curves for volcanic origin, dynamic equilibrium and land bridge origin scenarios. All plots were for island size $J = 10,000$ individuals and a difference log-series mainland immigration probability distribution. The columns correspond to different immigration rates and the rows correspond to different thresholds for what constitutes a ‘good immigration event’. For example, $\tau_l = 10$ means that a newly immigrating species must survive for 10 generations to be counted as a good immigration event.

DISCUSSION

We find that the NSIM at equilibrium produces almost exactly the straight lines for immigration and extinction rates that are also predicted under the simplest version of MacArthur and Wilson’s theory of island biogeography in which all species have equal immigration probabilities. This finding was robust to choices of parameter values, but only appears at equilibrium, so was not detected in earlier work that combined equilibrium and disequilibrium behaviour (Hubbell, 2010). It is likely that the linearity comes about because at equilibrium the species richness never drifts far, so we only see small and apparently linear sections of what are really much larger curves as a function of species richness. It is thus important to consider the disequilibrium behaviour of the system to fully understand immigration and extinction.

Despite these similarities to the ETIB, the NSIM of island biogeography generates a range of distinct quantitative predictions that could be tested empirically. First, the NSIM predicts particular patterns as islands approach equilibrium, reflected in distinct dynamics of immigration rates, extinction rates, and species abundance distributions. Second, the NSIM makes very different predictions for volcanic and land bridge islands. Third, the NSIM makes specific predictions

about temporal species turnover rates when islands are near equilibrium. We discuss these three predictions in more detail below.

The NSIM model predicts particular patterns as islands approach equilibrium. Indeed, the behaviour of the NSIM at disequilibrium is qualitatively different from that of the ETIB and reflects real biological processes involving the changing abundances of species (Fig. 4) that are rarely considered in the context of island biogeography. Different species abundance distributions can have the same species richness but different immigration and extinction rates. For example, more rare species would lead to higher extinction rates as rarity often precedes extinction. The only case where we envisage that abundance may not be correlated with extinction probability would be the complete sterilization of an island; even in the case of major disasters, a more abundant species has a greater chance of leaving some survivors.

In the volcanic origin case, extinction rates increased with species richness, but then peaked and decreased again before suddenly converging onto the straight line expected at equilibrium. Hubbell (2010) mentioned the first peak as the result of low immigration rates, although this was not shown in a graph. Here we find that the peak is not the exception as suggested, but rather it is a general rule across the

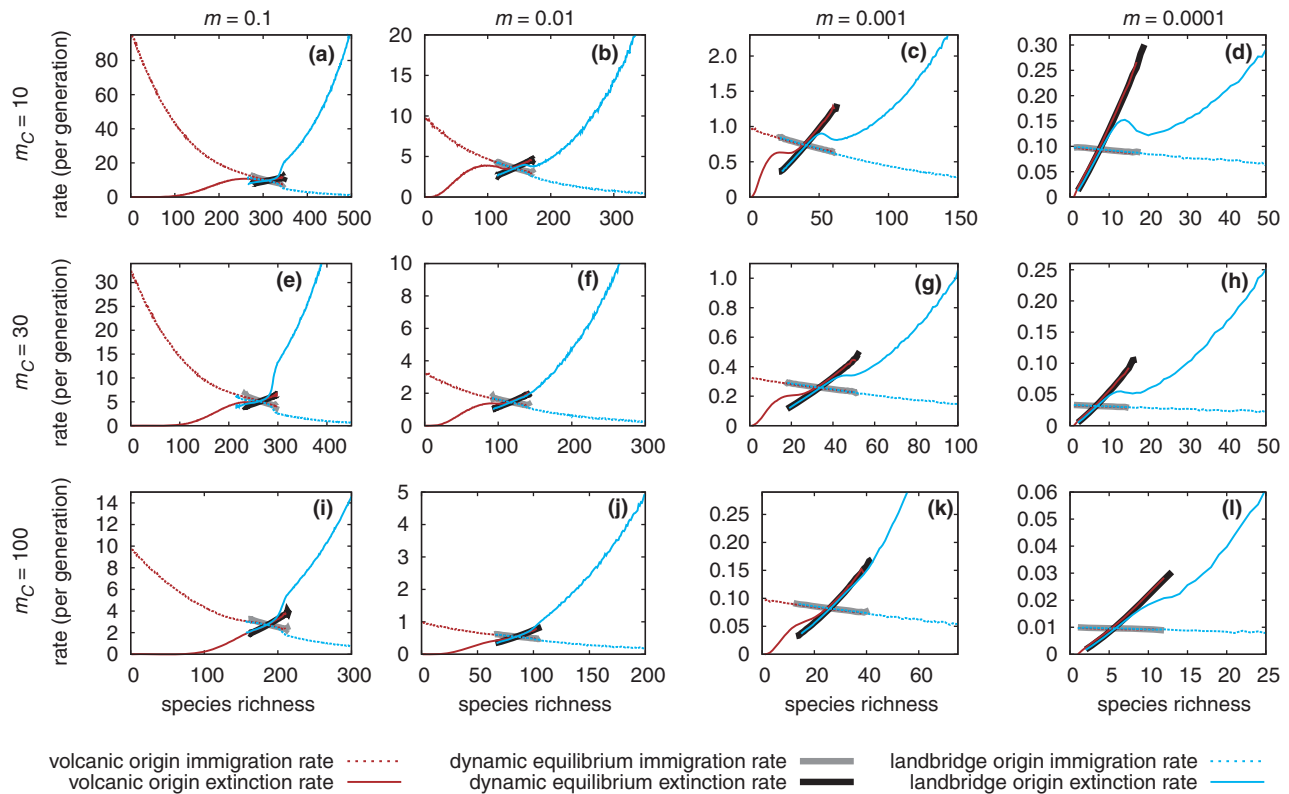


Figure 6 Clustered immigration results: each panel shows, for a different set of parameters, the immigration rate and extinction rate curves for volcanic origin, dynamic equilibrium and land bridge origin scenarios. All plots were for island size $J = 10,000$ individuals and a difference log-series mainland immigration probability distribution. The columns correspond to different immigration rates (m) and the rows correspond to different sizes of clustered immigration event. For example, $m_c = 30$ means that each immigrating species brings in 30 individual organisms of the same species.

majority of parameter space that only disappears under extremely high immigration values of $m = 0.5$, where immigration swamps the system and makes the interior peak undetectable.

The reason for the first interior peak is that newly immigrated species have an abundance of one and hence high chances of extinction after only a small time delay. The extinction rate as a function of species richness therefore increases from zero to a high level quickly, but ultimately becomes positively correlated with immigration because the newly immigrated species are mostly the ones going extinct. Empirical data do indeed seem to show that a burst of immigration is followed by a burst of extinction shortly afterwards, supporting the idea that the two could be correlated as our model suggests (Bush & Whittaker, 1993). Species richness is initially rapidly increasing, so it has already reached quite a high level in the short time delay between the first few immigration events and the extinction of the majority of those first species. Immigration and extinction then fall into step with one another, and extinction rates begin to decrease along with immigration, whilst species richness slowly increases. Similar non-monotonic patterns of immigration and extinction rates have been observed on Krakatau, where they were attributed to succession (Bush & Whittaker, 1991, 1993). Although it is clear that succession is

important on real world volcanic islands, here we show that even in the absence of succession, changing abundance distributions through time can still cause or contribute to non-monotonic extinction curves.

The sudden change in the extinction rate curve when it stops decreasing and converges to the equilibrium case is a feature of the convention that rates be plotted as a function of species richness rather than as a function of time (Fig. 2). Each point on the curve represents an average of the system across many cases of hitting exactly that species richness: some correspond to where species richness is on its way to the equilibrium value for the first time; others correspond to the case where the system is extremely close to equilibrium. The sudden turn in the extinction curve appears at the species richness where the number of readings taken at a time close to equilibrium outweighs the number taken during the earlier stages of approach to equilibrium. This transition happens extremely suddenly because the vast majority of near equilibrium readings are close to the equilibrium species richness and so a small increase in species richness can cause them to overwhelm the other readings. The land bridge approach to equilibrium also has a sudden turn in its extinction curve for the same reasons. Where each mainland species has the same abundance, the land bridge initial condition gives all species a high abundance and thus extinction

rate is initially zero and increases slowly because the extinction of any of these initially common species must be preceded by rarity and that takes time (Fig. 3i–l).

The immigration curves are in accord with MacArthur and Wilson's theory, having a curved and decelerating shape for mainland species immigration probabilities following a difference log-series. This is caused by the species absent from the island tending to be the ones that have a lower chance of getting there, as proposed by MacArthur and Wilson. We note that the differences in species immigration probabilities from the mainland could be explained entirely neutrally by differing abundances on the mainland (Hubbell, 2010), or non-neutrally involving different dispersal abilities. It is very easy to state in text, as MacArthur and Wilson did, that the model includes the effects of differences between species' dispersal abilities (and thus is non-neutral). In reality, however, the model is logically identical to one where all the species have the same dispersal abilities but different abundances on the mainland. Study of mainland species abundances, and the integration of those data into the model would be the only way to distinguish the effects of abundance and dispersal ability.

The ETIB and NSIM (at equilibrium) also differ dramatically in their predicted rates of turnover. The NSIM predicts turnover, immigration and extinction as *emergent properties* of dispersal and area. In contrast, the ETIB (in its best known form) predicts richness as an emergent property of immigration and extinction; thus it can essentially match any measured turnover rate with ease. It is conspicuous that per-generation species turnover rates predicted by the NSIM appear rather high (Figs 2–4). Measuring true rates of turnover empirically is, however, fraught with difficulties: predictions can be different by orders magnitude based on sampling interval, sample size and methodological efficiency (Lynch & Johnson, 1974; Simberloff, 1976; Diamond & May, 1977). Most real turnover unfortunately involves rare species, and these are the hardest to detect. We must therefore consider the possibility that empirical measurements of turnover are biased so that the original NSIM predictions of relatively high turnover are correct. This could come about either because of ambiguity in the definition of immigration (Lynch & Johnson, 1974) that can now be resolved with the protracted immigration model that models colonization rather than immigration, or because of sampling issues. For example, we may miss the colonization and subsequent extinction of a species due to infrequent surveys (Diamond & May, 1977); this is known as 'crypto-turnover' and it would influence both immigration and extinction rates. Another type of sampling error is 'pseudo-turnover' which refers to an already colonized species that is missed in one survey from a time series, leading to the possibly false conclusion that it went locally extinct and then re-colonized (Whittaker *et al.*, 2000). Pseudo-turnover, however, causes overestimation in real rates of turnover and that would not explain the high rates that our model predicts without sampling artefacts.

If the high turnover predicted by our model is incorrect, a more realistic immigration model is likely to resolve this. We considered the effects of clustered immigration, where species arrive through immigration with larger abundances from the start. This may reflect the immigration process, for example birds arriving as flocks, or it may implicitly reflect a rare species advantage of new immigrants. We note, however, that a truly accurate implementation of rare species advantage in a model would require the abundance of the species to influence the reproductive success of each individual and this would make the model non-neutral. We found that clustered immigration significantly lowered the turnover predicted by the model as well as altering the shapes of the immigration and extinction curves, making them closer to being monotonic and like those used by the ETIB.

Future work could implement land bridge removal and volcanic activity as gradual changes to island size or isolation (rather than sudden ones as in the present work). It will be valuable to understand the behaviour of the model during this period of gradual change. It would also be possible to include speciation in the model, which is likely to be important for modelling the most isolated islands, but less relevant for islands where local immigration remains the dominant input of new species (Rosindell & Phillimore, 2011). To consider speciation in this model would require two separate curves for species input: immigration and speciation. This has been considered in existing work (e.g. Lomolino, 2000; Chen *et al.*, 2011) albeit at the species level rather than at the individual level.

Succession might also be incorporated into future work by modelling each guild with a separate neutral model. The carrying capacity of a focal guild could vary, based on the growth patterns of the other guilds with which it interacts. We would expect such a model to predict that a sufficiently motile guild with short generation times would always be at equilibrium, but that the equilibrium itself is shifting slowly based on other factors. In contrast, less motile and longer-lived guilds may find themselves forever chasing a changing equilibrium level of species richness (Whittaker & Fernández-Palacios, 2007). Succession is expected to be important in the colonization of volcanic islands in particular (Whittaker *et al.*, 1989; Bush & Whittaker, 1991, 1993), and could cause an increase in total immigration rates over time rather than a decrease (Connell & Slatyer, 1977).

CONCLUSIONS

MacArthur and Wilson's theory revolutionized the field of island biogeography (MacArthur & Wilson, 1963, 1967) and inspired the unified neutral theory of biodiversity and biogeography (Hubbell, 2001). The predictions of neutral theory for immigration and extinction rates have not previously been understood, yet they are central to the unification of MacArthur and Wilson's work with ecological neutral theory. We have investigated the best-known neutral model (NSIM) and new variations of it in the context of MacArthur and

Wilson's ETIB. We find that when at equilibrium, the NSIM produces very similar immigration and extinction curves to the ETIB. In contrast the behaviour on approach to equilibrium is rich and unexpected, often qualitatively different to that expected by the ETIB, with immigration and extinction rates being non-monotonic functions of species richness that depend strongly on the initial conditions of the system. For example, immigration and extinction rates can be positively correlated in cases where most extinctions are of newly immigrated species that do not get the chance to colonize fully.

Immigration and extinction rates as a function of species richness can only give a restricted view of the complete dynamics of the system; they do not display time, or species abundances. The ETIB itself is similarly missing consideration of the species abundances, which are important because rarity usually precedes extinction. The NSIM can encompass the predictions of the ETIB and, with two possible new modes of immigration, can incorporate lower turnover rates and account for bias in the definition of turnover. We hope that this work will help to unite ecologically neutral theory with the ETIB, lead to more advanced individual-based island models and inspire further data collection and analyses on islands.

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REFERENCES

- Azovsky, A.I. (1988) Colonization of sand "islands" by psammophilous ciliates: the effect of microhabitat size and stage of succession. *Oikos*, **51**, 48–56.
- Bush, M.B. & Whittaker, R.J. (1991) Krakatau: colonization patterns and hierarchies. *Journal of Biogeography*, **18**, 341–356.
- Bush, M.B. & Whittaker, R.J. (1993) Non-equilibration in island theory of Krakatau. *Journal of Biogeography*, **20**, 453–457.
- Chen, X., Jiao, J. & Tong, X. (2011) A generalized model of island biogeography. *Science China: Life Sciences*, **54**, 1055–1061.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, **111**, 1119–1144.
- Diamond, J.M. & May, R.M. (1977) Species turnover rates on islands: dependence on census interval. *Science*, **197**, 266–270.
- Etienne, R.S., Alonso, D. & McKane, A.J. (2007) The zero-sum assumption in neutral biodiversity theory. *Journal of Theoretical Biology*, **248**, 522–536.
- Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*, **12**, 42–58.
- Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Hubbell, S.P. (2010) Neutral theory and the theory of island biogeography. *The theory of island biogeography revisited* (ed. by J. Losos and R.E. Ricklefs), pp. 264–292. Princeton University Press, Princeton, NJ.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69–80.
- Levine, J.M. & Rees, M. (2002) Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *The American Naturalist*, **160**, 452–467.
- Lomolino, M.V. (2000) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography*, **9**, 1–6.
- Losos, J.B. & Ricklefs, R.E. (2010) *The theory of island biogeography revisited*. Princeton University Press, Princeton, NJ.
- Lynch, J.F. & Johnson, N.K. (1974) Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. *The Condor*, **76**, 370–384.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254–283.
- Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, **14**, 552–560.
- Rosindell, J., Cornell, S.J., Hubbell, S.P. & Etienne, R.S. (2010) Protracted speciation revitalizes the neutral theory of biodiversity. *Ecology Letters*, **13**, 716–727.
- Rosindell, J., Hubbell, S.P. & Etienne, R.S. (2011) The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology and Evolution*, **26**, 340–348.
- Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J. & Etienne, R.S. (2012) The case for ecological neutral theory. *Trends in Ecology and Evolution*, **27**, 203–208.

- Schoener, T.W. (2010) The MacArthur–Wilson equilibrium model: what it said and how it was tested. *The theory of island biogeography revisited* (ed. by J. Losos and R.E. Ricklefs), pp. 52–87. Princeton University Press, Princeton, NJ.
- Simberloff, D.S. (1976) Species turnover and equilibrium island biogeography. *Science*, **194**, 572–578.
- Simberloff, D.S. & Wilson, E.O. (1969) Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, **50**, 278–296.
- Wennekes, P.L., Rosindell, J. & Etienne, R.S. (2012) The neutral–niche debate: a philosophical perspective. *Acta Biotheoretica*, **60**, 257–271.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Whittaker, R.J., Bush, M.B. & Richards, K. (1989) Plant recolonization and vegetation succession of the Krakatau Islands, Indonesia. *Ecological Monographs*, **59**, 59–123.
- Whittaker, R.J., Field, R. & Partomihardjo, T. (2000) How to go extinct: lessons from the lost plants of Krakatau. *Journal of Biogeography*, **27**, 1049–1064.
- Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Software package in C++.

BIOSKETCH

James Rosindell is a biodiversity theorist based at Imperial College London. He has particular interest in neutral models and how they can be applied to aid our understanding of macroecology and evolution. Recently, he has been working on island biogeography applications of these types of models. Rosindell was a visitor in the Harmon lab at the University of Idaho from July 2010 until August 2011.

Author contributions: J.R. conceived the ideas, wrote the software, collected the results and wrote the manuscript; L.J.H. gave support throughout, helped design the study, helped interpret the results, and contributed to the writing and revision of the manuscript.

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