

## Competition and introduction regime shape exotic bird communities in Hawaii

Javier G.P. Gamarra<sup>1,2,\*</sup>, José M. Montoya<sup>1</sup>, David Alonso<sup>1,2</sup> & Ricard V. Solé<sup>1,2</sup>

<sup>1</sup>ICREA-Complex Systems Lab, IMIM-UPF(GRIB), Dr. Aiguader, 80, 08003, Barcelona, Spain; <sup>2</sup>Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA; \*Author for correspondence (Department of Natural Resources, 103 Rice Hall, Cornell University, Ithaca, NY 14853, USA, e-mail: jgg25@cornell.edu; fax: +1-607-2550238)

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### Abstract

Complex combinations of historical and local-regional processes determine the assembly of ecological communities. We investigated such processes in the Hawaiian introduced avifauna, comprising 140 years of historical records of invasions and extinctions of birds. Here the particular introduction regime (i.e., colonization attempts and number of introduced species) and priority effects constitute the historical (and regional) component, and competition is the local component. These processes are theoretically supported by means of a Lotka–Volterra model of species competition, finding that changes in the specific introduction regime might result in different extinction dynamics. Both field data and model outcomes support the biotic resistance hypothesis, so that the invasibility of new incomers decrease with species richness. Finally, we found that the resistance to new invaders depends on the particular introduction regime. Thus, community assembly models built to predict the success of exotic species should consider more scenarios than random introduction regimes.

### Introduction

A great deal of processes have been suggested to understand what mechanisms produce the observed patterns in the assembly of ecological communities (see Weiher and Keddy 1999 for a compilation). Species availability from regional species pools is a fundamental constraint for local assemblages in many communities, so that local species richness is highly correlated with the number of species in the surrounding region (Cornell 1999). Some processes deal with the temporal sequence of invasions from species pools as a determinant of species composition (Drake 1991; Sait et al. 2000; Hewitt and Huxel 2002). Priority effects (i.e., species introduced ear-

lier are more prone to persist) are also suggested as an assembly rule (Drake 1991; Lockwood et al. 1999). Other proposed mechanisms include: (1) the physiological tolerance of the exotic species to the new abiotic environment (Williamson and Brown 1986; Blackburn and Duncan 2001b); (2) species-specific traits such as morphological dispersion, sexual dimorphism or body sizes (Simberloff and Boecklen 1991; McLain et al. 1995; Roy et al. 2001); and (3) local species interactions, mainly competition and the eventual dominance of weak interactions (Diamond 1975; Moulton and Pimm 1983, 1985; Case 1990, 1991; Kokkoris et al. 1999; McCann 2000). This complex set of ecological processes frustrates any attempt to predict which species are likely to

invade or be lost from particular ecosystems, and also complicates testing if species richness is a barrier to new incomers (i.e., biotic resistance hypothesis, *sensu* Elton 1958), a particularly relevant current issue (Lodge 1993; Mooney and Hobbs 2000; Hewitt and Huxel 2002).

A large effort to provide good data for testing hypothesized processes using simulation models has given rise to the so-called community assembly theory (Diamond 1975; Post and Pimm 1983; Case 1990, 1991; Drake 1990, 1991; Drake et al. 1993; Law and Morton 1996; Law 1999; Weiher and Keddy 1999). Despite the number of studies providing real data, both in the field (Diamond 1975; Benke 1978; Lockwood et al. 1999; Blackburn and Duncan 2001a) and through microcosm experiments (Morin 1984; Drake et al. 1993; Sait et al. 2000), long-term assemblage studies in the field are scarce (Law 1999; Weiher and Keddy 1999; van Ruijven et al. 2003). Among the best documented examples is the historical record of the human-introduced avifauna in the Hawaiian islands (Moulton and Pimm 1983; Simberloff and Boecklen 1991). These introductions started as far back as 1796 and continue in the present day, mainly through accidental escapes to the wild involving at least, 140 bird species (Moulton and Pimm 1983; Simberloff and Boecklen 1991; Moulton et al. 2001).

Different processes have been proposed to explain the observed patterns in the Hawaiian exotic avifauna. Early studies suggested that observed extinction patterns of birds were associated with competitive interactions among introduced species (Moulton and Pimm 1983, 1985; Moulton 1985). These authors found that, as species richness increased, extinction rates increased non-linearly, matching the predictions of the island biogeography theory (MacArthur and Wilson 1967). Later re-analysis by Simberloff and Boecklen (1991) suggested that Moulton and Pimm's results were an artifact because of pseudoreplication problems, offering an alternative explanation: the all-or-nonpattern. This hypothesis states that species succeed or fail because of the species-specific features, so no community-level process, such as species richness, determines the assembly (Simberloff and Boecklen 1991).

Here we re-analyze bird introductions in the Hawaiian Archipelago and compare them with

the outcomes of a simply modified, Lotka-Volterra competitive model, reproducing the particular sequence of introductions over 140 years with Simberloff and Boecklen's original data. We wish to answer several questions aiming to find alternatives to the mechanisms subjacent under "all-or-none" schemes: (1) Are there priority effects? (2) If so, are they also supported by a competitive framework? (3) Are there hidden correlations in the invasion-extinction dynamics stressing the importance of invasion intensity? (4) If so, is the introduction regime affecting the extinction outcomes under a competitive framework? (5) Is biotic resistance still supported under different introduction regime scenarios?

## Materials and methods

### *The introduced Hawaiian avifauna series*

We used data from Simberloff and Boecklen (1991) involving the introduction of 69 species of Passeriforms (perching birds) and Columbiforms (pigeons) over a period of 139 (1850–1988) years in the six larger islands of the Hawaiian Archipelago (Figure 1). Larger data sets are also available (Moulton et al. 2001), but they only account for dates of first introductions, giving no possibility to compute extinction (or failure) rates at short time scales. Following previous studies on this exotic avifauna (Moulton and Pimm 1983; Simberloff and Boecklen 1991; Keitt and Marquet 1996), we have considered Passeriforms and Columbiforms as a single species pool, assuming that all species can interact despite phylogeny. The data contain the approximate dates of introduction and extinction for each species on each island. Introductions were direct (human-driven) on each island (2/3 of the total), or indirect via natural dispersal of birds between islands. Exotic species were introduced and persist in disturbed lowland habitats, whereas native birds remain in undisturbed highland areas, so that there is little direct interaction between exotic and native avifaunas (Moulton and Pimm 1983; Keitt and Marquet 1996). We considered each island separately as well as the whole Archipelago by pooling all the islands as a single highly connected ecosystem. The latter can be done because of

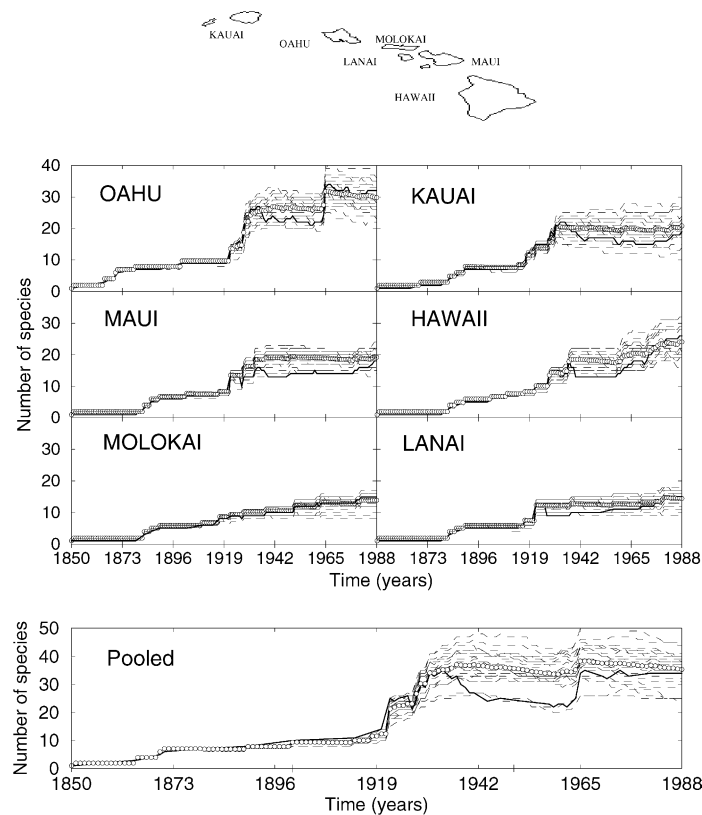


Figure 1. Community size of the introduced Hawaiian avifauna in the period 1850–1988 in the six major island considered separately and in the Archipelago as a whole (pooled). Thick lines: original field data after Simberloff and Boecklen (1991); dashed lines: 25 simulation runs based on the original LVM model; open circles: average trajectory of the simulation runs.

large spatial correlations due to high rates of dispersal between islands, as Moulton (1993) suggested at least for seven of the most abundant species.

#### The model

We used a standard Lotka–Volterra model (LVM) of species competition (Case, 1990, 1995; Kokkoris et al., 1999). If  $N_i$  is the population size of species  $i$  (here  $i = 1, \dots, S$ ), then:

$$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{\sum_j^S \alpha_{ij} N_j}{K_i} \right) \quad (1)$$

where  $r_i$  and  $K_i$  stand for growth rate and carrying capacity of the  $i$ th species, respectively,  $S$  is the number of species in the community, and  $\alpha_{ij}$  is the per capita interaction strength (we assumed

full intraspecific competition, that is,  $\alpha_{ii} = 1$ ). This is a multiparametric model, but its complexity can be strongly reduced by means of appropriate transformation. By non-dimensionalization, the simplified equations become

$$\frac{dx_i}{dt'} = \frac{r_i x_i}{r_m} \left( 1 - \sum_j^S \alpha_{ij} x_j \right) \quad (2)$$

where  $r_m = \max\{r_i; i = 1, \dots, P\}$ ,  $P$  is the total number of species of the potential pool, and  $t' = t/r_m$  is scaled time. This simple step ensures that the multiple  $K_i$  do not affect the dynamics and the new equation now accounts for a realistically plausible time scale, where all populations  $x_i \in [0, 1]$  (Gurney and Nisbet 1998).

Growth rate estimates from average trends based on the most reliable surveys in many of the recently invaded states from the conterminous

US were used to assign a value of  $r_m = 0.4/\text{yr}^{-1}$  (Sauer et al., 2000). This apparently high value is reasonable not only for species spreading over vast areas, but also for many newly arrived invaders, which are often good colonizers. We first considered any pair of species as competitively related with probability  $C$ , among those  $P = 69$  species from the pool (Simberloff and Boecklen 1991). We selected a connectivity  $C = 0.5$ . This assumption may seem too simplistic, but it relaxes the lumping condition between both bird families (in which only granivores may compete). We have also tried other values of connectivity and, in some range of values  $C \in [0.2, 1]$  the system adequately fits the data, even at lower  $r_m$  values. Furthermore, because most of the species are phylogenetically related at the level of family (Moulton 1993), the network of competitors could indeed be highly connected. We tested simulations with other values by heuristically maximizing the goodness of fit for all the islands and the results are robust for a variety of values of the two-dimensional parameter space with  $C$  and  $r_m$ . Interaction strengths  $\alpha_{ij}$  were drawn from a uniform distribution  $\alpha_{ij} \in [0, 1]$  (Gilpin and Case 1976, 1990).

Because our time scale was meant to be realistic, we could introduce in the simulation the exact introduction regime (i.e., temporal sequence of invasions and number of species introduced) that every island (and the whole Archipelago) experienced, from the first introduction considered (1850). This realistic constraint assumes that there is no time left for this competitive system to achieve stability, standing in a permanent transient state. Thus, we intentionally avoided testing for stability every time we introduced a new species (Case 1995; Hewitt and Huxel 2002). We assumed that new species enter into the system in very small populations  $x_i = 0.001$  (Moulton and Pimm 1983; Case 1990, 1991), the same threshold under which species are considered extinct. We also simulated an introduction regime in which introduction attempts were randomly taken from a uniform distribution. Extinction dynamics are compared between the real introduction and the uniform regime. In doing so, we test (1) to what extent introduction regime determines patterns of extinction through time, and (2) the robustness

of priority effects under different regimes of species introduction.

#### *Persistence and invasibility measures*

To test the presence of priority effects we analyzed species-specific persistence times by species and island. We defined a persistence index for every species and introduction attempt in an island as  $\Pi_{i,t} = p_{i,t}/(T - \omega_{i,0})$ , where  $p_{i,t}$  stands for the persistence time of every species  $i$  after every introduction event at time  $t$ ,  $T$  is the time of the whole series in the island, and  $\omega_{i,0}$  is the time a species  $i$  was first introduced the island. This dimensionless quantity reflects in summary the probability of survival of any species until the end of the census. In addition, we sought patterns of cross-correlation between introduction and extinction events to check for short-term responses by species failures following introduction attempts. The appearance of a significant  $k$  time lag for extinctions following invasions was then the variable used to compute the probability that a species survived less than  $k$  years after its introduction, both for real data and simulations. The selection of a 10-year interval is due to the fact that extinctions follow introductions with a significant delay of 10 years in the historical record (see Results). We pooled the number of species going extinct before  $k$  years, by computing

$$\Pr\{p_{i,\Omega} < k\} = \frac{\sum_{t=\Delta}^{\Delta+\delta} \sum_{i=1}^{I_\Omega} s\{p_{i,t} < k\}}{I_\Omega} \quad (3)$$

where  $I_\Delta$  stands for the number of invaders at time  $\Omega$ , which comprehends the interval  $\{\Delta, \Delta + \delta\}$  and  $\delta$  is the pooling time necessary for sampling purposes. We chose  $\delta = 10$  for the computation of extinction rates as in Keitt and Marquet (1996).  $s\{p_{i,t} < k\}$  has a value 1 if the condition is true and 0 otherwise. Other authors have used similar dimensionless measures in the computation of extinction rates (Moulton and Pimm 1983; Keitt and Marquet 1996). This measure will reinforce the positive or negative evidence of priority effects: if these probabilities increase through time, priority effects must be playing an important role in community assembly.

In order to test the biotic resistance hypothesis (Elton 1958) we used an invasibility measure based on Case's criterion for the success of any invader species (Case 1991). In particular, we studied the evolution of invasibility in relation to community size (i.e., number of species) and time, using the results of the model contrasted with a uniform, random pattern of introductions. Thus, if invasibility decreases with time or community size, resistance to newly introduced species increases. We assume that for every new species entering the system it will locally succeed only if its growth rate is positive (Case 1991). The invasibility condition for the  $i$ th invader is expressed as

$$\Gamma_i = \begin{cases} 1 & : 1 - \sum_j^S \alpha_{ij} x_j - x_o > 0 \\ 0 & : \text{otherwise} \end{cases}$$

where  $x_o$  is the minimum population threshold for extinction, which we assumed to be the same for all species.  $S$  is the total number of species in the community. Therefore, our invasibility criterion for the community is expressed as

$$\Upsilon_i = \frac{\sum_{i=1}^{P-S} \Gamma_i}{P-S} \quad (4)$$

where  $P-S$  defines the number of species, not present in the community, but available in the pool: the number of potential invaders.

We also measured invasibility under a uniform introduction regime. The comparison between real and random, uniform regime allows us to test the dependence of extinction patterns and biotic resistance on the introduction regime.

## Results

An overall pattern of increase in species richness is observed for each island and the whole Archipelago, although specific sequences of introductions and extinctions are different between islands (thick lines in Figure 1). Oahu and Hawaii were the islands with the highest number of introductions.

### *Correlation structure in the invasion regime*

The first half of the period studied corresponds to a continuous and slow process of introductions.

The second half was characterized by fast introductions and extinctions, interrupted by periods of stasis, with two main invasion episodes involving numerous new species in the 1920's and 1960's. This pattern was observed in all the islands except Molokai, where sudden introductions with many species invading at once were not observed (Figure 2a). Large invasions were followed by relatively large extinctions. Cross-correlation analysis showed that extinctions followed invasions after a significant delay of  $k=10$  years in Oahu, Hawaii, and the pooled data (Figure 2b). In Kauai, extinctions appear after 15 years. However, as a general rule, we used  $k=10$ , which is the time lag used to later compute the probability of persistence of a species after its introduction. Although this pattern could be due to the artificial nature of the historical reconstruction of data, specially in assigning extinction dates (Moulton and Pimm 1983), it strikingly matches the lifespan of any invader population that fails to succeed when it enters in

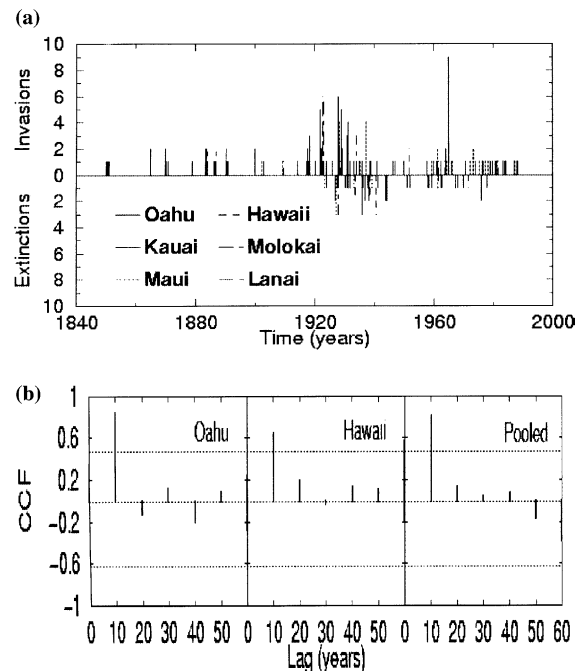


Figure 2. (a) Series of invasion and extinction events in the six main islands over the period investigated. (b) Cross-correlations between invasions and extinctions for the two main islands and the pooled data. Data were time-pooled in 10-year groups.

small numbers and is not able to reproduce before being outcompeted (Klimkiewicz 2000).

#### *Assembly processes involved*

We found evidence of three assembly processes regulating the introduced Hawaiian avifauna: competition, priority effects and introduction regime. Our competition model reproduced diversity dynamics (i.e., species richness and extinctions) observed in real data in each of the observed islands and in the pooled data (dashed lines in Figure 1). This gives theoretical support to previous studies emphasizing the importance of competitive interactions in this community (Moulton and Pimm 1983; Moulton 1993).

#### *Priority effects and competition*

Priority effects are observed both in real data and in our simulations. The first species introduced tend to become established and defeat the later ones. The persistence index  $\pi_{i,t}$  for Oahu, Hawaii and the pooled Archipelago, clearly distinguished two periods in time (Figure 3). In the first time period, every species entering the island has survived to present (i.e.,  $\pi_{i,t} = 1$ ). This observation is shared with the rest of the islands (with only two exceptional species, *Alauda arvensis*, Linnaeus and *Parus varius*, Goul, invading Kauai in 1870 and 1890, respectively). The second half is characterized by the presence of many species with persistence index  $\pi_{i,t} < 1$  (most of them with  $\pi_{i,t} < 0.4$ ), mainly those invading during large introduction events. Priority effects are also supported by looking at the probabilities of species persistence for less than 10 years (Figure 4). These probabilities increase with time and community size, both in field and simulated data with

real introduction regime. As most extinctions occur within a 10 year interval (Figure 2b), this result shows that the probability of a species becoming established diminishes with time and species richness, and it is very high in early assembly stages (Benke 1978). Furthermore, we observed that priority effects are also present when a random, uniform introduction regime is used in our model, so they are not only a consequence of a particular introduction regime.

#### *Introduction regime*

The specific introduction regime influences observed extinction dynamics. Using pooled data, the introduction regime follows a power law with an exponent  $\theta \approx -1.25$  ( $r^2 = 0.71$ ,  $P < 0.002$ , see inset in Figure 5a), which is far from a uniform natural rate of colonization attempts assumed in biogeography theory (MacArthur and Wilson, 1967). Frequency distributions of extinction rates (i.e., number of extinctions per species per year pooled in 10 years intervals) show a power law decay with almost the same exponent as our simulation results ( $\theta \approx -0.91$ ,  $r^2 = 0.9$ ,  $P < 0.001$ ) (Figure 5a). By contrast, when a random, uniform introduction regime is considered in our model, extinction rates follow a Poisson distribution  $\Pr\{E\} = e^{-\lambda} \lambda^E / E!$  (Kolmogorov-Smirnov  $d = 0.024$ ,  $P < 0.001$ ), where  $E$  is extinction size. Thus, random invasions are followed by constant rates of extinction events with average  $\lambda \approx 4.3$  (Figure 5b).

Large invasion events are responsible for observed differences in extinction dynamics between real and random, uniform introduction regimes. In these events, the perturbation is so extreme that it diverts the community from its route to equilibrium, creating instabilities, so

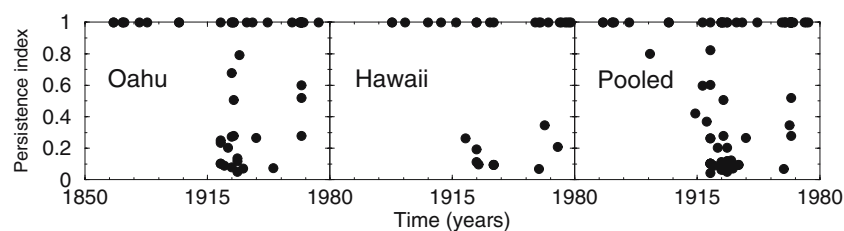


Figure 3. Persistence index for every species entering either any of the two main islands or the Archipelago as a whole.

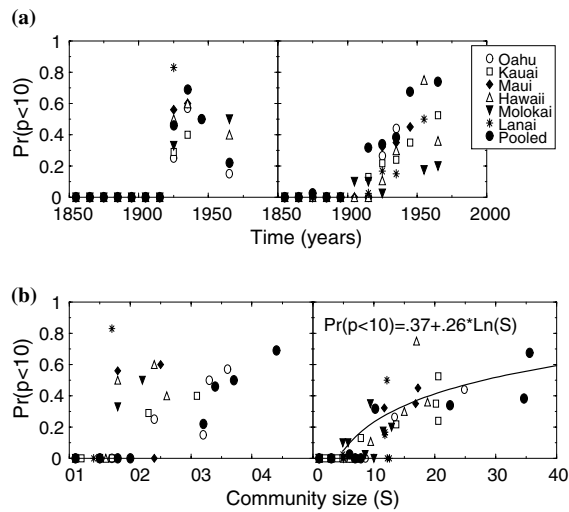


Figure 4. Species-specific probabilities of persisting less than 10 years in the islands as a function of (a) time, and (b) community size. Left: original field data. Right: LVM simulations. Observe the presence of marked thresholds in both analysis and the asymptotic behavior of these probabilities in islands with higher number of species.

long transients are needed to return to equilibrium, and some species were not able to survive under such instabilities (Case 1995). Thus, we observed that species invading in these events showed different persistence times, from immediate failures to full replacements (Case 1990).

Some authors have identified differences between non-Passeriforms and Passeriforms that

might justify their separation in this kind of analysis (see Moulton 1993). Although Columbiforms are poorly represented in the Hawaiian assemblage ( $19/69 = 27.5\%$ ), it has been argued that patterns in introduction success among Columbiforms are determined mostly by species-specific properties instead of competitive interactions (Simberloff and Boecklen 1991; Moulton 1993). For that reason, we have also performed both field data analysis and simulation considering only Passeriforms. The results are very similar to those including all the species. There is no change in the role of competition, priority effect or introduction regime.

#### Invasibility

Biotic resistance to new invaders is observed in our simulations both when a real and a random, uniform introduction regime are considered, although their relationship with time and community size is different (Figure 6). In Oahu, there is a departure from  $Y_t = 1$  at  $S \approx 7$  (Figure 6a), similar to the threshold found for persistence probabilities (Figure 4b). When introductions are driven by a random distribution, invasibility decreases exponentially with time (in agreement with Case 1991), whilst when introduction regime follows a power law, no typical statistical distribution is obtained, but a clear decrease in invasibility is also observed (Figure 6b). Here again large invasion events are responsible for these

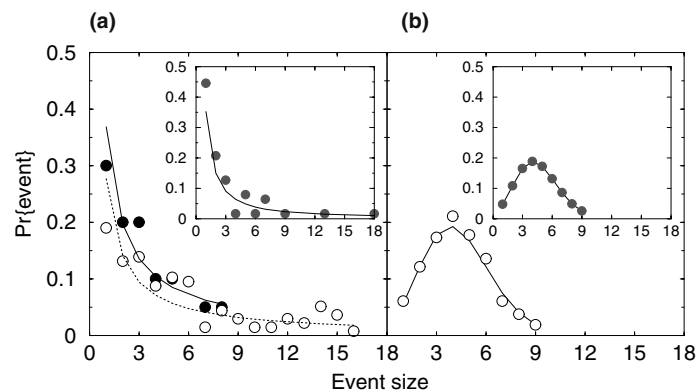


Figure 5. Distribution of extinction event sizes for different introduction regimes. (a) Real introduction regime, modified from Keitt and Marquett (1996). Filled circles: real data. Empty circles: simulation outcome. (b) Uniform, random introduction regime (see text). Insets: distributions of introduction regimes. Simulation results define averages over 20 realizations for every introduction regime.

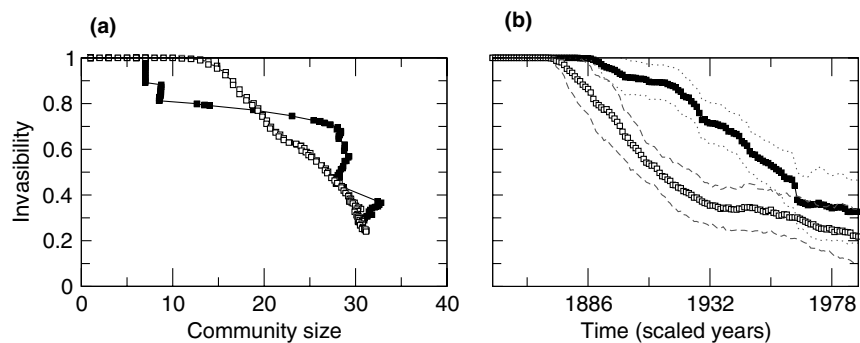


Figure 6. Community invasibility related to (a) community size and (b) time, for simulation outcomes in Oahu Island with different introduction regimes. Black squares correspond to the real introduction regime. Open squares correspond to random invasions. Standard deviations are drawn as dotted lines in the original, real invasions. Dashed lines draw standard deviations in the uniform, random invasion regime.

differences, because the power-law regime implies that, in some cases, species enter later in sudden pulses that destabilize the overall dynamics of populations, triggering sudden extinction episodes that allow new colonizations to take place. However, randomly distributed invasions seem to depend only on community size, since the system is not forced by sudden pulses of invasion attempts.

## Discussion

The dynamics of the Hawaiian introduced avifauna result from the combination of historical (and regional) components, and species local interactions. Introduction regime and priority effects constitute the historical and regional component, whereas competitive interactions constitute the local process affecting this assemblage. The importance of competition has been previously suggested using bill-length differences (BLDs), showing that pairs of species that coexist and survive tend to have larger BLDs than do pairs in which one species goes extinct (Moulton 1985; Moulton and Pimm 1985). Competition may not necessarily be the cause of priority effects, since many species that could be outcompeted when all the species arrive simultaneously can in fact persist if they enter early and increase in abundance. In long-term assembly dynamics as that reported here, competition and priority effects may play crucial roles in different stages, depending on the specific introduction regime.

The central argument of the all-or-none pattern is that species always succeed or fail independently of what and how many other species are present in the community (Simberloff and Boecklen 1991). For example, sexually dichromatic birds were less likely to become established in Oahu (McLain et al. 1995). Furthermore, widespread species were more successful in Hawaii than those species of limited range (Moulton and Pimm 1985; Moulton et al. 2001). Introduction history alone has been reported as a predictor of introduction outcomes, supporting all-or-none patterns, and consequently, the ability to predict which species will succeed (Simberloff and Boecklen 1991). However, our work presents a critique to the “all-or-none” pattern as a general mechanism determining which exotic bird species failed or succeeded in Hawaii. We have shown here that community invasibility (a common way of measuring the success of new incomers) highly depends on how many species are present on the community, and the invasion sequence and timing. These may thrive the appearance of priority effects, which otherwise may be disrupted by counterintuitive, indirect effects following species introductions in competitive communities (Case 1995; Hewitt and Huxel 2002). This seems to be the case in the exotic bird Hawaiian data, where priority effects are observed, but some species go extinct many years after a large introduction event.

Priority effects are extensively reported in field experiments on different taxonomic groups of animals: odonates (Benke 1978; Morin 1984),



coral reef fishes (Shulman et al. 1983), flies (Shorrocks and Bingley 1994) and anurans (Wilford and Alford 1985). They are also found in introduced Passeriform assemblages on another oceanic islands (Lockwood et al. 1999). Conversely, Lockwood et al. (1999) did not find evidence of priority effects in Oahu when failed or succeeded introductions of Passeriforms before 1981 were compared to the mean numbers of species present. This contrasts with our findings for the pooled data and individual islands, including Oahu, that support priority effects because the probability of persisting less than 10 year increases with time and community size (Figure 4). Models of competition (Case 1991, Case 1995) and trophic interactions (Drake 1990, 1991; Luh and Pimm 1993) have also provided evidence of priority effects. In these models different invasion sequences (the order in which species enter into the community), were simulated, obtaining communities with different species composition where species introduced earlier are almost always present. Due to low initial competition, first introduced species attain population sizes sufficiently large to resist later introductions. When the community achieves a certain number of species, later introductions may fail, and extinctions take place.

Except invasion sequence (i.e., specific order of species introduction taking into account species identity), other consequences of species introductions have received little attention. For instance, Ward and Thornton (2000) found that the length of the interval between species arrivals affects the likelihood of the establishment of late incomers. Our results suggest that the particular introduction regime (i.e., number of colonization attempts and number of species introduced in a particular period) play a key role in the assembly of ecological communities, and models should not consider introductions as random events, but should consider more realistic regimes, especially when introductions are human-driven (Blackburn and Duncan 2001b). Furthermore, appropriate modeling of non-uniformly driven invasion regimes must not be based on the foundations of local or global stability analysis, which is intended to check whether coexistence of species is feasible at long terms (Post and Pimm 1983; Case 1995; Law and Morton 1996). In order to account for

transients and short-term extinctions we need to track instabilities driven by large introduction episodes, and dynamical equilibrium must be defined at long-term time scales. Then we agree with Hewitt and Huxel (2002) on the unstabilizing effect of multiple species attempting to establish at one time.

Both data and model outcomes support the biotic resistance hypothesis (Elton 1958), and partially agree with the typical pattern of invasibility found in the theoretical literature based on uniform introduction regimes: as species richness increases, biotic activation barriers appear (Hall and Ehler 1979; Case 1990, 1991; Rejmanek 1996; Levine and D'Antonio 1999). However, invasibility under the real introduction regime showed strong, sudden transitions in relation to community size, because of large invasion episodes. The reason for this is both species richness and the dynamics of population numbers. Some species are not able to withstand large instabilities and many of them decrease in population numbers with the new arrival of strong and weak competitors (Case 1995). If, at the introduction time, some species do not achieve a sufficiently large number of individuals to resist other competitors, extinctions will appear in a long range of times following invasion, and persistence times will achieve large variances, from rejection failures to full replacements (Case 1990). Thus, the strength of biotic resistance to new invaders relies not only on the combination of total density and community size (Pimm 1991). The size of the population entering the system, and the size of the populations of the species already present in the community plays a very important role in shaping diversity (Griffith et al. 1989; Case 1995; Duncan 1997; Blackburn and Duncan 2001a), especially when communities are not in equilibrium, which implies a new paradigm on island biogeography (Lomolino 2000). Regarding this issue, Keitt and Marquet (1996) hypothesized that self-organized critical (SOC) dynamics could be driving the dynamics in the exotic Hawaiian Avifauna. They found power-law distributed extinction rates and extinction thresholds, which could be found also in SOC-driven systems. Indeed, we are dealing with a non-equilibrium community and community-level properties seem

to arise non-trivially from species interactions. However, our results show that: (1) there is a dominant correlation in time between introduction and extinction events; and (2) the power-law distribution of extinctions follows accordingly a similar distribution of invasion events. Thus, there is not constant forcing followed by long-correlations, as SOC dynamics implies, so we can not support Keitt and Marquet's hypothesis.

Finally, it is important to stress that our model, although not fully neutral, is the simplest, most general competition model we have found which accounts for short-term extinctions and species diversity. By contrasting human-induced with random introduction regimes, we highlight the importance of the specific sequence of introductions in competing communities. Our results suggest that large extinction events only take place under multiple species invasion models, giving support to Hewitt and Huxel's (2002) argument that biotic resistance under random invasion assumptions may indeed be relaxed by other factors.

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### References

- Benke AC (1978) Interactions among coexisting predators: a field experiment with dragonfly larvae. *Journal of Animal Ecology* 47: 335–350
- Blackburn TM and Duncan RP (2001a) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography* 28: 927–939
- Blackburn TM and Duncan RP (2001b) Determinants of establishment success in introduced birds. *Nature* 414: 195–197
- Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA* 87: 9610–9614
- Case TJ (1991) Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* 42: 239–266
- Case TJ (1995) Surprising behavior from a familiar model and implications for competition theory. *American Naturalist* 146: 961–966
- Cornell HW (1999) Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience* 6: 303–315
- Diamond JM (1975) Assembly of species communities. In: Cody ML and Diamond JM (eds) *Ecology and Evolution of Communities*, pp 343–444. Harvard University Press, Cambridge, Massachusetts
- Drake JA (1990) The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147: 213–233
- Drake JA (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137: 1–26
- Drake JA, Flum TE, Witteman G, Voskuil T, Hoylman AM, Creson C, Kenny DA, Huxel GR, LaRue CS and Duncan JR (1993) The construction and assembly of an ecological landscape. *Journal of Animal Ecology* 62: 117–130
- Duncan RP (1997) The role of competition and introduction effort in the success of passeriforms birds introduced to New Zealand. *American Naturalist* 149: 903–915
- Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. University of Chicago Press, Chicago, Illinois
- Gilpin ME and Case TJ (1976) Multiple domains of attraction in competition communities. *Nature* 261: 40–42
- Gurney WSC and Nisbet RM (1998) *Ecological Dynamics*. Oxford University Press, Oxford
- Griffith B, Scott JM, Carpenter JW and Reed C (1989) Translocation as a species management tool: status and strategy. *Science* 245: 477–480
- Hall RW and Ehler LE (1979) Rate of establishment of natural enemies in classical biological control. *Bulletin of the Entomological Society of America* 25: 280–282
- Hewitt CL and Huxel GR (2002) Invasion success and community resistance in single and multiple species invasion models: do the models support the conclusions? *Biological Invasions* 4: 263–271
- Keitt TH and Marquet PA (1996) The introduced Hawaiian avifauna reconsidered: evidence for self-organized criticality. *Journal of Theoretical Biology* 182: 161–167
- Klimkiewicz MK (2000) *Longevity Records of North American Birds – Version 2000.1*. Patuxent Wildlife Research Center. Bird Banding Laboratory, Laurel, Maryland
- Kokkoris GD, Troumbis AY and Lawton JH (1999) Patterns of species interaction strength in assembled theoretical competition communities. *Ecology Letters* 2: 70–74
- Law R (1999) Theoretical aspects of community assembly. In: McGlade JM (ed) *Advanced Ecological Theory: Principles and Applications*, pp 143–171. Blackwell, Oxford
- Law R and Morton RD (1996) Permanence and the assembly of ecological communities. *Ecology* 74: 762–775

- Levine JM and D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26
- Lockwood JL, Moulton MP and Balent KL (1999) Introduced avifaunas as natural experiments in community assembly. In: Weiher E and Keddy P (eds) *Ecological Assembly Rules. Perspectives, Advances, Retreats*, pp 108–129. Cambridge University Press, Cambridge
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133–137
- Lomolino MV (2000) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography* 9: 1–6
- Luh HK and Pimm SL (1993) The assembly of ecological communities: a minimalist approach. *Journal of Animal Ecology* 62: 749–765
- MacArthur RH and Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey
- McCann KS (2000) The diversity-stability debate. *Nature* 405: 228–233
- McLain DK, Moulton MP and Redfearn TP (1995) Sexual selection and the risk of extinction: an analysis with introduced birds. *Oikos* 74: 27–34
- Mooney HA and Hobbs RJ (eds) (2000) *Invasive Species in a Changing World*. Island Press, Washington DC
- Morin PJ (1984) Odonate guild composition: experiments with colonization history and fish predation. *Ecology* 65: 1866–1873
- Moulton MP (1985) Morphological similarity and the coexistence of congeners: an experimental test with introduced Hawaiian birds. *Oikos* 44: 301–305
- Moulton MP (1993) The all-or-none pattern in introduced Hawaiian Passeriforms: the role of competition sustained. *American Naturalist* 141: 105–119
- Moulton MP and Pimm SL (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist* 121: 669–690
- Moulton MP and Pimm SL (1985) The extent of competition in shaping an experimental fauna. In: Diamond J and Case T (eds) *Community Ecology*, pp 80–97. Harper and Row
- Moulton MP, Miller KE and Tillman EA (2001) Patterns of success among introduced birds in the Hawaiian islands. *Studies in Avian Biology* 22: 31–46
- Pimm SL (1991) *The Balance of Nature?* University of Chicago Press, Chicago, Illinois
- Post WM and Pimm SL (1983) Community assembly and food web stability. *Mathematical Bioscience* 64: 169–192
- Rejmanek M (1996) Species richness and resistance to invasions. In: Orians G, Dirzo R and Cushman H (eds) *Biodiversity and Ecosystem Processes in Tropical Forests*, pp 153–172. Springer-Verlag, Berlin
- Roy K, Jablonsky D and Valentine JW (2001) Climate change, species range limits and body size in marine bivalves. *Ecology Letters* 4: 366–370
- Sait SM, Liu w-C, Thompson DJ, Godfray HCJ and Begon M (2000) Invasion sequence affects predator–prey dynamics in a multi-species interaction. *Nature* 405: 448–450
- Sauer JR, Hines JE, Thomas I, Fallon J and Gough G (2000) *The North American Breeding Bird Survey, Results and Analysis 1966–1999 – Version 98.1*. USGS Patuxent Wildlife Research Center, Laurel, Maryland
- Shorrocks B and Bingley M (1994) Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *Journal of Animal Ecology* 63: 799–806
- Shulman MJ, Ogden JC, Ebersole JP, McFarland WM, Miller SL and Wolf NG (1983) Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64: 1508–1513
- Simberloff D and Boecklen W (1991) Patterns of extinction in the introduced Hawaiian avifauna: a reexamination of the role of competition. *American Naturalist* 138: 300–327
- van Ruijven J, De Deyn GB and Berendse F (2003) Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecology Letters* 6: 910–918
- Ward SA and Thornton IWB (2000) Chance and determinism in the development of isolated communities. *Global Ecology and Biogeography* 9: 7–18
- Weiher E and Keddy P (1999) *Ecological Assembly Rules. Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge
- Wilbur HM and Alford RA (1985) Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* 66: 1106–1114
- Williamson M and Brown KC (1986) The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society of London B* 314: 505–522