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# Research article

# Species reintroduction and community-level consequences in dynamically simulated ecosystems

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Global biodiversity, and its associated ecosystem services, are threatened due to species extinctions. Reintroducing locally extinct species may be a partial solution to this problem. However, the success and possible consequences of any artificial reintroduction will depend on its ecological community, and the reaction of that community to the species' extinction and reintroduction. Mathematical models can offer useful insights by identifying the key features of communities and reintroduced species most likely to result in successful reintroductions.

Here we simulated extinctions and reintroductions for a range of theoretical food webs generated using an established bioenergetics model. This allows the probability of successful reintroductions to be quantified as a function of two important ecological factors: the connectance of the food web, and of the time between extinctions and reintroductions.

Reintroduction success is measured across an ensemble of 1796 simulated communities, with connnectances of 0.05, 0.15 and 0.3, using three criteria: presence of the reintroduced species in the final community, unchanged species richness in the final community compared to the pre-extinction persistent community and the complete restoration of the community (including both species richness and equilibrium biomass distributions).

Although only 12 reintroduced species fail to re-establish according to minimal criteria, the process of extinction and reintroduction frequently has a large effect on the community composition. Increasing time to reintroduction increases both the probability of species loss, and equilibrium biomass change in the community. Proportionally, these community-level impacts occur more frequently when the reintroduced species is a primary producer or top predator. These results indicate that ignoring broader measures of reintroduction success could seriously underestimate the impact of reintroductions on the ecological community. These quantitative results can be compared to empirical literature and may help reveal which factors are most important to the success of reintroductions.

**Key words:** extinction, food web, niche model, nonlinear bioenergetic dynamic model, reintroduction, connectance

## Introduction

### Biodiversity loss and the science of reintroduction biology

Global biodiversity loss is a well-documented phenomenon that threatens ecosystems worldwide. There is strong evidence that biodiversity is positively correlated with certain ecosystem services (Cardinale *et al.*, 2012). Reintroductions, defined as 'the intentional movement and release of an organism inside its indigenous range from which it has disappeared' (IUCN/SSC, 2013), are therefore becoming increasingly attractive in conservation.

Seddon, Armstrong and Maloney (2007) detailed the history of reintroduction biology, dating from the 1907 reintroduction of American Bison (*Bison bison*) to Oklahoma. Success stories, such as the reintroduction of Grey Wolves to Yellowstone (Ripple and Beschta, 2012), show that such efforts can benefit an area's ecology and management. Other issues, such as changing public attitudes to zoos, increased governmental conservation action and a desire to re-establish or restock hunting populations have led to an increase in reintroduction programmes since the 1990s (Seddon, Armstrong and Maloney, 2007).

Despite this practical activity, the science underpinning reintroduction biology is still developing and lacks the mature theoretical framework seen in sister fields such as invasion biology (Seddon, Armstrong and Maloney, 2007). Some general rules exist describing, for example, the importance of maintaining genetic diversity in reintroduction populations (Ren *et al.*, 2014), or using more individuals in reintroduction attempts (Godefroid *et al.*, 2011). However, most work published in the field is limited to case-by-case predictions (Armstrong and Ewen, 2002; Bennett *et al.*, 2013; Davidson and Armstrong, 2002).

Williams (1997) suggested three stages characterizing the maturation of a science, summarized by Seddon, Armstrong and Maloney (2007) as '(1) observation guided by intuition, tradition, and guesswork; (2) organization of those observations into coherent categories, the exploration of observations for patterns, and the clear description of patterns; and (3) recognition of the underlying causes of patterns and formulation of theories that lead to testing of predictions deduced'. Seddon, Armstrong and Maloney (2007) concludes that reintroduction biology is advancing into stage two, but could progress faster by drawing on theory from other disciplines.

Computer modelling will be important in the development of the science of reintroduction ecology (Armstrong and Seddon, 2008). However, although population viability analysis models can be used in individual reintroduction projects (Nolet and Baveco, 1996; Seddon, Armstrong and Maloney, 2007), no predictive models of general reintroduction success have been proposed.

Here, we describe a modelling framework to predict the success of reintroductions based on the delay between extinction and reintroduction, and the trophic identity of the reintroduced species. This method has been adapted from work modelling invasion success (Romanuk *et al.*, 2009).

### Modelling ecological dynamics

Dynamic network models have been used to describe and quantify many complex biological phenomena, ranging from gene pathways and chemical reactions to climate change and ecological communities (Proulx *et al.*, 2005). Such models have been used in invasion biology to predict invasion success based on general community network and invasion species variables (Romanuk *et al.*, 2009). This was accomplished by generating independent realizations of dynamic communities, randomly parameterized from a range of empirically based values using the so-called niche model of generating complex food webs (Williams and Martinez, 2000). These communities were simulated deterministically, using coupled ordinary differential equations (ODEs), following established methods (Brose, Williams and Martinez, 2006; Williams and Martinez, 2004; Yodzis and Innes, 1992).

The niche model of generating complex food webs improves upon May's random model (May, 1972) and Cohen's cascade model (Cohen, Briand and Newman, 1990). It successfully estimates the central tendency of empirical data better than the other models, and with generally smaller normalized errors of the empirical web properties on the means of those properties in the model (Williams and Martinez, 2000).

The bioenergetics model used here is reconstructed from Romanuk *et al.* (2009). It incorporates a density dependent functional response in the interspecific feeding relationships (Holling, 1959b). We use a modified type II response, referred to as a 'type II.2', intermediate between type II and type III responses (Holling, 1959a,b; Williams and Martinez, 2004). The model lacks Allee effects (Courchamp, Berec and Gascoigne, 2008) and stochastic elements; instead its deterministic nature allows the general trends underlying reintroduction success to be identified.

### Aims

By modelling extinction and reintroduction, we aimed to answer the following questions:

(i) How does time to reintroduction (the duration between extinction and reintroduction of the subject species) affect the success of reintroductions, as measured according to three criteria:
   (a) Reintroduction subject species re-establishment: is the species present in the community at the end of the experiment?
   (b) Successful restoration of the original species richness: does the subject species or other species go extinct?
   (c) The successful restoration of the equilibrium biomasses of all of the community's species?

(ii) How does web connectance affect the success of reintroductions?

(iii) How does the reintroduced subject species' trophic level affect the success of reintroduction?

(iv) If species are lost from communities during the simulations:

    (a) Is there a relationship between the trophic group of the species lost and the trophic group of the reintroduced species?

    (b) When are species lost from communities? Does this happen while the subject species is extinct or is it a consequence of the reintroduction?

## Methods

Food webs were generated at three levels of expected directed connectance ($C$), $C = 0.05$, $C = 0.15$ and $C = 0.3$; actual directed connectance was also recorded. Directed connectance, the probability that any two species in the food web have a feeding relationship, is equal to $L/S^2$, where $L$ is the number of feeding relationships between species ($S$) (Martinez, 1991) and is expected to be similar to the expected connectance in generated webs. Communities with different levels of connectance may react differently in simulations, and therefore data is split by the level of expected connectance during analysis.

Simulations were implemented as follows:

Initially, random food webs were generated using the niche model (Williams and Martinez, 2000) with expected $C$ of 0.05, 0.15, or 0.3, as detailed in Appendix 1. Then, each species was assigned an initial biomass drawn from a uniform random distribution from 0.5 and 1. These were kept identical in all simulations. Each network's interaction dynamics were simulated using the bioenergetic model until time $t = 2000$, in line with previous work (Romanuk et al., 2009), however, resulting dynamics typically settled around an equilibrium point within a few hundred time steps. For each persistent food web, five surviving species were randomly selected as the subjects of the reintroduction simulations. Each reintroduction simulation systematically selected one of these species and removed it from the food web. The dynamics of the new webs were simulated for times to reintroduction of 10, 100, and 1000, respectively i.e. the extinct species was introduced at either $t = 2010$, $t = 2100$, or $t = 3000$. The species was reintroduced with a biomass drawn from a uniform random distribution of 0.5–1. The dynamics of the new reintroduced webs were then simulated to $t = 4010$, $t = 4100$ or $t = 5000$, depending on the time to reintroduction used.

### The bioenergetic model of community dynamics

The dynamic model used in this work follows Romanuk et al. (2009) and builds upon earlier work (Brose, Williams and Martinez, 2006; Martinez, Williams and Dunne, 2006;

McCann and Hastings, 1997; McCann, Hastings and Huxel, 1998; McCann and Yodzis, 1995; Williams and Martinez, 2004; Yodzis and Innes, 1992).

The change in biomass of species $i$ ($B_i$) over time is calculated using equation (2.1):

$$\frac{dB_i(t)}{dt} = G_i - x_i B_i + \sum_{j=1}^{n} x_i y w_{ij} F_{ij} B_i(t) - \sum_{j=1}^{n} \frac{x_j y w_{ji} F_{ji} B_j(t)}{e}$$

(2.1)

Equation (2.1) can be broken into four terms that represent the net primary production rate of basal species, the metabolic loss of species $i$, and the sums of the gains from resources and losses from consumers respectively.

The net primary production of species ($G_i$) equals $r_i B_i(t)[1 - B_i(t)/K_i]$, where $r_i$ is the intrinsic growth rate of species $i$ that is zero for all non-basal species, $B_i(t)$ is the biomass of species $i$ at time $t$, and $K_i$ is the carrying capacity of species $i$. In the term representing metabolic loss, $x_i$ is the mass specific metabolic rate.

In the final two terms, representing gains and losses from resources and consumers, $y$ is a constant describing the maximum rate of assimilation of one species by another per unit metabolic rate, $w_{ij}$ is a term indicating the relationship between species $i$ and $j$, equal to 1 if $i$ consumes $j$, otherwise equal to 0, $e$ is a constant describing the efficiency with which biomass consumed by one species is converted to its own biomass. By dividing the final term by $e_{ji}$ the biomass assimilated by consumer $j$ is converted to biomass lost by species $i$.

$F_{ij}$ is the realized fraction of the maximum ingestion rate of predator species $i$ consuming prey species $j$ and is detailed in equation (2.2). It is a non-dimensional functional response that may depend on the consumer biomass ($B_j$) and the biomass of $i$'s resource species ($B_k$). $B_0$ is the half saturation density—'the resource density at which half the saturation ingestion rate is attained' (Yodzis and Innes, 1992).

$$F_{ij} = \frac{B_j^{1+q}}{B_0^{1+q} + \sum_{k=1}^{n} w_{ik} B_k^{1+q}}$$

(2.2)

The values of the above terms were assigned fixed parameters in Romanuk et al. (2009) as estimated from empirical studies: $r_i = 1$ for basal species or 0 for non-basal species; $K_i = 1$; $x_i = 0.5$; $y = 6$; $e_{ij} = 1$; $q = 0.2$; and $B_0 = 0.5$ (Brose, Berlow and Martinez, 2005; Brose, Williams and Martinez, 2006; Yodzis and Innes, 1992).

Using this model bioenergetic dynamics were simulated from $t = 0$ to $t = 2000$ using Matlab (Version 8.3.0.532 (R2014a)). The scripts used are found in the appendix. Initial biomasses, drawn from a uniform random distribution between 0.5 and 1, were assigned to species at $t = 0$. Species were considered to have gone extinct if their biomass dropped

below $B = 10^{-10}$. To reduce the computing time of the experiments to a practically feasible duration, community biomass values were checked at regular intervals for extinction. This means that it is possible for a species' biomass to have dropped below the extinction threshold briefly, and yet not be removed. Detailed examination of a subset of individual time series indicated that this happens very rarely, if at all, and therefore does not affect the results presented here.

In fewer than 8% of simulations the script used to simulate bioenergetics was unable to calculate the dynamics due to the limits of the Matlab function 'ODE45' when the value of $B_i$ rapidly approached 0. This can occur before initial transients decay in the early stages of the simulation, or after the abrupt change due to extinction or reintroduction of a subject species. When this error occurred new initial biomasses were generated for the species, which fixed the issue in almost all cases. A few webs had to be rejected when five different biomass allocations did not prevent the error, but this occurrence was so rare as to leave the statistical results unchanged.

## Simulating extinction and reintroduction

At $t = 2000$, five surviving species from each web were randomly selected to be removed and subsequently reintroduced. Each species was simulated separately with three different times to reintroduction of $t = 10$, 100 and 1000. Individually for each subject species, at $t = 2000$ the subject's biomass was changed to 0. The network's dynamics were simulated using three different times to reintroduction of 10, 100, and 1000, until $t = 2010$, $t = 2100$, or $t = 3000$. At this point the subject species biomass was changed to a value drawn from a uniform random distribution between 0.5 and 1 to simulate reintroduction. The network's dynamics were then simulated until $t = 4010$, $t = 4100$, or $t = 5000$, for time to reintroduction value of 10, 100 and 1000, respectively. In this way, three simulations were run for each of the five subjects of the 40 webs at each level of expected connectance.

Reintroductions at a biomass of 0.1 and 0.0001, simulated from reintroduction at $t = 3000$ to $t = 5000$ were conducted to determine whether reintroduction biomass has an important effect on reintroduction success in our models.

## Evaluating reintroduction success

The success of reintroduction was judged on three criteria: firstly, the presence of the subject species at the end of the simulation; secondly, the absence of a decline in species richness in the final community when compared to the community before subject species extinction was simulated and lastly, the absence of a change of over 5% in biomass of any of the species in the final community when compared to the stable community prior to subject extinction.

These criteria of success are not mutually exclusive; in fact, loss of the subject species will cause both other criteria of success to fail as well. Similarly, the loss of any species will change the final biomass of that species by over 5% from the stable community. Other thresholds of biomass change were considered at 1%, 10% and 50% change in the biomass of any one species. These all resulted in qualitatively identical conclusions about the effect of reintroduction on the biomass equilibrium of the community. A change of 5% was chosen as it captures small, meaningful changes in species biomass, but is less sensitive to fluctuations of very small biomasses that may occur near equilibrium.

Data are analysed by comparing standard error of the mean (s.e.m.) value of a subset of data. Cases where standard error bars do not overlap indicate where differences in the simulation data may have a non-random cause. Because simulation data are generated as independent realizations of randomly parameterized dynamic communities, an analysis based on $p$-values is inappropriate; arbitrarily small $p$-values can emerge from statistically uninteresting effects, simply as a result of the large sample number (James, Pitchford and Plank, 2012, 2013).

## Results

### Dynamically persistent webs

The proportions of different trophic groups in persistent webs, as summarized in Table 1, show that as expected connectance increases the prevalence of intermediate species within the communities also increases. The increase

**Table 1.** The trophic composition, directed connectance and species richness of persistent webs at $t = 2000$, $n$ is the number of food webs generated at each level

| Connectance | $n$ | Proportions in persistent webs | | | Mean directed connectance | Mean species richness of persistent webs |
| | | Basal | Intermediate | Top | | |
|---|---|---|---|---|---|---|
| 0.05 | 40 | 0.389 | 0.423 | 0.188 | 0.0648 (0.0125 s.d.) | 22.08 (3.06 s.d.) |
| 0.15 | 40 | 0.269 | 0.693 | 0.038 | 0.1682 (0.0272 s.d.) | 19.35 (4.35 s.d.) |
| 0.3 | 40 | 0.178 | 0.816 | 0.007 | 0.3288 (0.0407 s.d.) | 19.73 (4.40 s.d.) |
| Total | 120 | 0.278 | 0.644 | 0.078 | | |

in intermediate species prevalence at higher levels of connectance reduces the prevalence of basal and top species to the point that most $C = 0.3$ webs contain no top species.

The directed connectance of the food webs generated was expected to vary from expected connectance due to the random community assembly processes, and because webs with a lower connectance are more likely to contain species or loops that match the criteria for web rejection. The values of directed connectance (Table 1) show that all groupings of expected connectance are distinct, despite $C = 0.05$ webs varying from their actual directed connectance by more than one standard error. The average biomass of species in persistent webs was 0.0585.

**Table 2.** The relative frequency of subject species trophic grouping

| Connectance | Trophic group | Simulations |
|---|---|---|
| 0.05 | Basal | 333 |
| | Intermediate | 176 |
| | Top | 90 |
| 0.15 | Basal | 219 |
| | Intermediate | 348 |
| | Top | 33 |
| 0.3 | Basal | 180 |
| | Intermediate | 408 |
| | Top | 9 |

## Successful reintroduction of the subject species

The final number of simulations included in the analysis for each level of connectance was 599, 600, and 597 simulations at $C = 0.05$, 0.15, and 0.3, respectively, with each of the three times to reintroduction being represented by around 200 simulations. The proportion of subject species of each trophic group is reported in Table 2. Full details can be found in the supplementary information.

The initial aim of this work was to determine what factors affect extinction and reintroduction subject species successfully re-establishing in their communities, indicated by presence of the subject species in the final community. In all but 12 cases, the subject species successfully reintroduced according to this measure.

The 12 simulations where reintroduction species failed to re-establish concerned only four subject species, each of which failed to reintroduce at all durations of time to reintroduction. Three of the subjects were part of webs where $C = 0.15$, and one where $C = 0.3$. All were intermediate species.

## Other measures of reintroduction success

A positive relationship between connectance and reintroduction success can be observed, both when success is measured using species richness and equilibrium biomass change. There is also a negative relationship observable between time to reintroduction and reintroduction success using these two measured of success. This relationship remains when the three levels of expected connectance are considered separately (Fig. 1).

The trophic group of the reintroduced species can also affect reintroduction success. When success is measured by
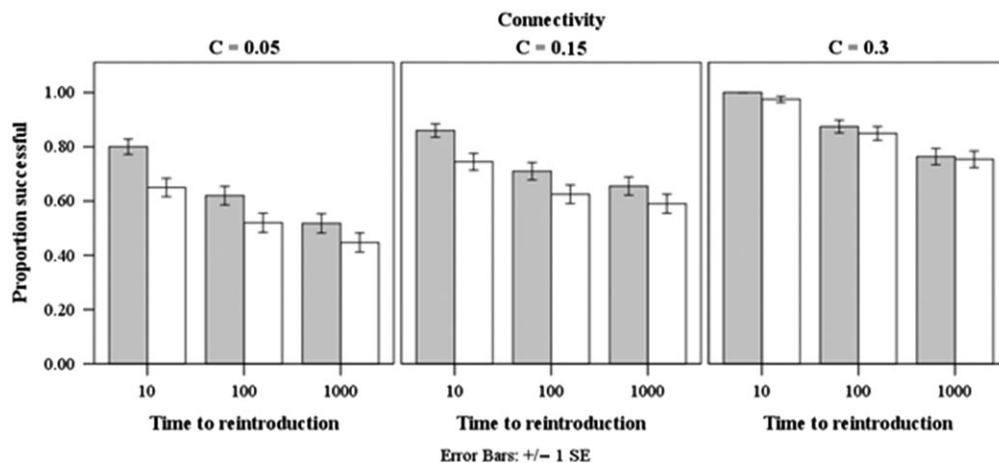


**Figure 1.** Reintroduction is more likely to be successful in more connected ecosystems, and if carried out soon after the initial extinction. Figure shows the proportion of successful reintroductions for each duration of time to reintroduction and connectance combination. Grey bars measure success in terms of secondary extinctions, white bars in terms of change to equilibrium biomasses. Error bars are $\pm$ 1 standard error of the mean.

species richness, basal and top species reintroductions generally have lower rates of success than intermediate species reintroduction, in that basal species have a lower success rate than intermediate species by one standard error at $C = 0.05$. This grows to a two standard error difference at $C = 0.15$ and $C = 0.03$. Although top and intermediate success is indistinguishable at $C = 0.05$, intermediate species are more successful at $C = 0.15$ and $C = 0.3$ by one standard error (Fig. 2).

When success is measured by a change in the web's equilibrium biomass, intermediate species have generally higher rates of success compared to top species (they differ by one standard deviation at $C = 0.05$ and 0.15, and by two standard deviations at $C = 0.03$). When compared to basal species this difference is similar, corresponding to one and two standard deviations at $C = 0.15$ and 0.3, respectively. Basal and top species are only meaningfully different at $C = 0.3$ where basal species are more successful by a difference of over two standard deviations (Fig. 2).

In no simulation was a basal species present in the community at $t = 2000$ lost in the final community. This is likely to be due to the simplicity of the model and its underlying deterministic population dynamics. The only way basal species could go extinct in this model is extreme over-predation or manual removal, and so the removal of predator species will never cause extinction. No convincing relationship could be found between trophic group of the reintroduction subject and the proportion of species lost belonging to each trophic group (Fig. 2), aside from the lack of basal species loss.

When basal species are the subject of reintroductions, the mean species loss, of 0.607 (0.0463 s.e.m.), is higher than when the subject species is either an intermediate species, with a mean species loss of 0.207 (0.0202 s.e.m.) or top species, with a mean species loss of 0.993 (0.1772 s.e.m.). This is true at all levels of expected connectance. The relationship

between intermediate and top species at different levels of expected connectance is variable.

Simulations carried out with lower reintroduction biomasses of 0.1 and 0.0001 (each consisting of 596 simulations), at time to reintroduction of 1000, did not vary meaningfully from the results reported for higher reintroduction biomasses.

Species reintroduced in this model have been limited to a reintroduction biomass drawn from a uniform random distribution from 0.5 to 1. To test whether this influenced the results, the 598 reintroductions for $t = 1000$ were re-simulated at low reintroduction biomass ($B = 0.1$ and $B = 0.0001$) and produced only superficial differences at every level of reintroduction success. No additional species failed to reintroduce. Given the mean biomass of persistent communities ($B = 0.0585$), a reintroduction biomass of 0.1 bridges the gap between the mean biomass of persistent communities and the reintroduction biomass of 0.5, which we have used to keep our work in line with Romanuk *et al.* (2009). The reintroduction biomass of 0.0001 is a relatively low biomass compared to the mean biomass of persistent communities and addresses concerns that our simulations fail to simulate real reintroductions at low biomasses. These results strongly suggest that in these deterministic models of species reintroduction, reintroduction biomass has a minimal effect in shaping the final community composition and equilibrium biomass and Romanuk *et al.*'s choice of reintroducing species with a biomass between 0.5 and 1 was justified.

## Discussion

As anticipated, the longer a species was removed from an ecological community, the lower the probability that it could be successfully reintroduced without impacting the wider community. We found a positive relationship between
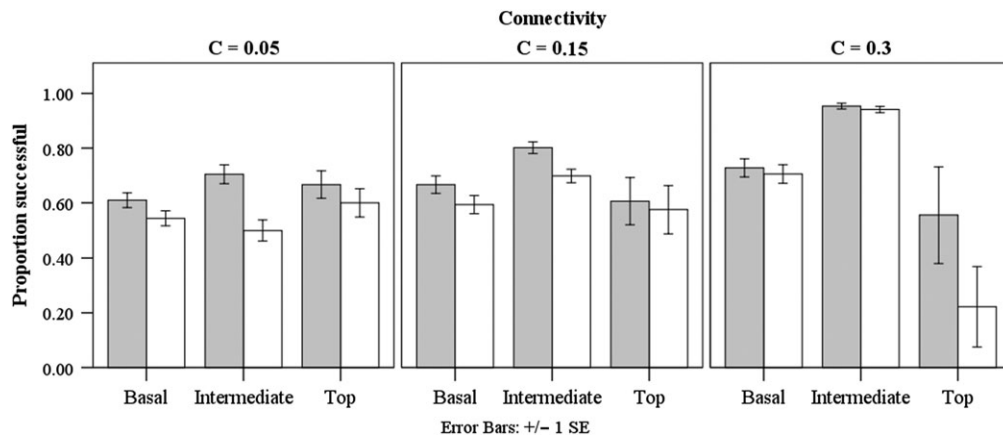


**Figure 2.** Reintroduction is more likely to be successful when the subject is a trophically intermediate species. Figure shows the proportion of successful reintroductions for each subject trophic group and connectance combination. Grey bars measure success in terms of secondary extinctions, white bars in terms of change to equilibrium biomasses. Error bars are ± 1 standard error of the mean.

connectance and proportion of successful reintroductions, as measured by species richness and biomass equilibrium. More connected webs also lost fewer species on average. These findings agree with other theoretical work suggesting that more connected webs are more robust to species removal (Camacho, Guimera and Amaral, 2002; Dunne, Williams and Martinez, 2002).

Although these results fail to show a relationship between the time to reintroduction and reintroduction species success, the study identifies important relationships between community-level measures of success and time to reintroduction, web connectance, and trophic grouping of the reintroduced species.

If the subject of an extinction and reintroduction is a basal or top species, the probability that the community will recover to the same species richness or biomass equilibrium is lower than if the subject species is an intermediate species. This is consistent across all levels of connectance examined in this study. Intermediate reintroduction subject simulations have the lowest values of species loss at all levels of expected connectance. It is notable that these results corroborate the findings of some extinction models (Borrvall, Ebenman and Jonsson, 2000; Eklof and Ebenman, 2006) and is consistent with arguments both for a bottom up and top-down determination of species richness.

Apart from the lack of any basal species loss during the simulations, there is no evidence to suggest that the species lost from communities are selected non-randomly from top and intermediate species groups. However, due to the prevalence of intermediate species in the food webs (Table 1), especially at higher values of connectance, it would be difficult to detect non-random loss of intermediate and top species. Studies suggest a higher number of top species should have become extinct due to top predator vulnerability (Sanders, Sutter and van Veen, 2013). In our simulations the predators in general were more vulnerable, and no basal species went extinct.

Species richness of persistent communities at $t = 2000$ was lower in $C = 0.3$ and $C = 0.15$ than in $C = 0.05$ (Table 1); however, there was overlap within one standard deviation. This suggests that connectance does not affect persistent community species richness and is consistent with some studies of connectance and species richness (Fox and McGrady-Steed, 2002). However, it does not fit with the hyperbolic connectance relationship (Chen and Cohen, 2000), or inverse relationship suggested in other work (Keitt, 1997; Laird and Jensen, 2007).

For models to be useful, they must be presented simply and clearly. The results of both Romanuk et al. (2009) and Williams and Martinez (2000) are difficult to replicate without ambiguity. For example, it is unclear whether top species include cannibalistic species, or only species that have no predators. These two definitions are not identical, and in our simulations they lead to slightly different success results. Similarly, it is not clear whether Romanuk et al. (2009)

removed trophically identical or disconnected species as in Williams and Martinez (2000). The MATLAB scripts for our simulations are included in the supplementary information for the sake of transparency.

Although modifications to the niche model have been suggested (Allesina, Alonso and Pascual, 2008; Cattin et al., 2004), Romanuk et al. (2009) argued that their original model maintained the most accurate fit to empirical data (Williams and Martinez, 2008). However, the model is unable to simulate webs with a connectance equal to or greater than 0.5 and can have difficulty simulating webs with connectance approaching 0.5. Moreover, it tends to create food webs with less variability and more intervality than those found in empirical systems (Romanuk et al., 2009). The variable $r_i$ in the niche model is also drawn from a restricted $\beta$ distribution where $\alpha = 1$. Williams and Martinez (2000) state that this is to ease calculation difficulty. The consequences of allowing $\alpha$ and $\beta$ to vary (so long as the expected value of $2C$ is maintained) are currently unstudied.

The food webs are constructed and simulated with regard to the feeding relationships of species. The models do not incorporate other ecological interactions that may not be directional, such as mutualisms that benefit both species. The term 'extinction' has been used throughout this work. However, given that the species is later reintroduced, at worst this 'extinction' refers either to the extinction of a species in the wild, or to a local extinction. Extinction, in the sense of this work, is a state where the species in question is no longer interacting trophically with the other species in its native community. Equally, reintroduction refers only to the return of that species to its native community. The population dynamics observed in this work typically occur at time scales on of the order of 10 time steps. Therefore, in regard to the dynamics of the system, the three times to reintroduction can be thought of as:

$t = 10$: the system has very been recently affected by the removal of a single species, but many subsequent effects of this extinction (e.g. secondary extinctions) have yet to occur.

$t = 100$: the system is beginning to equilibrate, and secondary extinctions may have occurred, but the community is still changing and has not reached an equilibrium. Species loss can still be prevented by reintroduction in principle, but much of the damage is already done.

$t = 1000$: the system has now reached, or is very close to, a new equilibrium point.

In the broadest terms, in a terrestrial community operating at annual time scales it would be appropriate to think of $T = 10$, 100 and 1000 corresponding to reintroductions after times of 1, 10 and 100 years, respectively.

The discrepancy between the absolute success rates of these theoretical reintroductions and the lower success rate of real reintroductions (Godefroid et al., 2011; Jule, Leaver and Lea, 2008) may be due to the simplicity of the bioenergetics model,

in that it ignores possible stress, low genetic diversity among other factors. Despite this, the fact that consistent and practically interpretable trends emerge from the simulations ought to provide useful general insight.

The simulations presented here assume that, given a food web and a set of parameters, the community dynamics are deterministic. Factors such as environmental and demographic stochasticity, and non-random drivers such as evolution, mean that real communities may be in a constant state of disequilibrium. It may be argued that over short time scales, and for large populations, a deterministic mean-field dynamics may operate, but this ought not to be regarded as self-evident (Van Kampen, 2007).

## Author's biography

Justin Byrne is a Masters student at the University of York, currently researching avian communities in the Albertine Rift. Previously he studied Biology (with a year in industry) at the University of York. He spent a year in industry at Kew's Millenium seed bank and then conducted this work as a dissertation project. He designed research, conducted research, analysed data, and wrote the paper. He has primary responsibility for the final content. Jon Pitchford is a Reader in mathematical ecology at the University of York. Jon designed research, and contributed to the analysis, writing, and revision of this work where specialist knowledge of mathematics was required.

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