

Multiple Life-History Stage Competition and its Effect on Coexistence.

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Abstract

Explaining the long-term coexistence of many species in a complex ecosystem has been an important topic in both A-Life and ecology for several decades. Neutral and niche theories have been developed in parallel to explain ecological patterns of coexistence. Among the niche theories, trade-offs between species seem to play important roles in the mechanism of most models proposed so far. One of the many trade-off approaches to explain coexistence within trophic levels explores the scenario of species having two developmental stages existing in different ecological niches. Previous work has shown that such multi-stage models can sustain many species with inter-specific competitive coefficients larger than intra-specific ones for one of the stages, but the effect of such scenarios on the possible combinations for coexistence in the parameter space has not been explored. Here, we build on previous work by considering the effect of adding more stages to the competition model and analysing the relative sizes of the basins of attraction leading to coexistence. Computational simulations and Monte Carlo methods were used to analyse each number-of-life-stages case. The results show an increase in the number of coexistence cases between one and three stages. For more than three stages coexistence cases are reduced in relation to the parameter space due to the averaging effect of multiple competitive coefficients. The implications of such results could offer a potential explanation for coexistence patterns in ecology and adaptive ones in evolutionary biology.

Introduction

The successful modeling of open-ended complexity in real ecosystems has long been a target for A-Life researchers (Channon and Damper, 2000; Channon, 2008; Shao and Ray, 2010; Ray, 1994). One of the great challenges for these models is achieving the long-term coexistence of a diverse collection of species. All too often the model collapses into a mono-culture or a small trophic cycle. One of the many simplifications that such models typically employ is to consider only a single life-stage for each of the species involved: there are only tadpoles, for example, and not both tadpoles and frogs. Here we show that including the possibility of multiple life stages can actually *promote* the persistent coexistence of multiple species, as Moll and Brown (2008)

have previously argued. Furthermore, we show that there is an optimal number of life stages to achieve long-term complexity, and that this number is a function of how quickly the environment fluctuates.

In current ecological literature a great number of theories and models have been developed in order to explore different biodiversity patterns (Chesson, 2000). Species coexistence models are concerned primarily with the basic problem of resource allocation among different species and the principle of competitive exclusion. These models attempt to generate *stable* coexistence over extended periods of time and they contrast with models of *unstable* coexistence which are concerned with mechanisms for delaying competitive exclusion by minimizing the differences between species fitness (Chesson, 2000; Moll and Brown, 2008). All *stable* coexistence models operate by establishing directly or indirectly a greater degree of intra-specific competition compared to inter-specific competition (Chesson, 2000).

Multiple Life-History Stage models are a type of stable coexistence model that depend on trade-offs. Here, the trade-off happens between different developmental stages of two or more species. In particular, these trade-off models show that the apparent coexistence of a great number of species is explained by the presence of many life-history stages with associated ecological niches. This is a phenomenon that has not yet been considered in the A-Life literature, and so in the current paper we draw on the relevant ecological literature to develop a simple dynamical-systems model of competing species with multiple life stages.

During their development, organisms of several species go through a series of phenotypic changes that affect the way they interact and exploit their environment (Werner and Gilliam, 1984). Drastic examples of these cases can be seen in insects (Dopman et al., 2007), amphibians (Werner and McPeck, 1994; Werner et al., 1995; Werner and Anholt, 1996) and fish (Arendt and Wilson, 1997). But similar interpretations can be extrapolated to plants with their different seed, sprout, juvenile, and adult stages, and plankton where different fluid dynamics and predatory pressures affect their interaction with the medium (Padisák et al., 2003). From

an evolutionary point of view, these differences between developmental stages allow juveniles to avoid direct competition with adults of the same species, and following Gillian's rule, evolution can move the population towards niche shifts where the ratio of mortality over individual growth is minimized (Werner and Gilliam, 1984; Claessen and Dieckmann, 2002). This process of adaptive niche shift during individual development is known as ontogenetic niche shift. From a competitive point of view, the picture that such systems show is one with an age-structured population where different species in the same guild and with similar developmental stages go through a stepped competition sequence where some individuals might do better than others at different stages (Moll and Brown, 2008; Fujiwara et al., 2011). The second diagram in figure 1 explains this approach for the simplest case of two species and two stages.

Previous work on this approach includes Moll and Brown (2008) and Fujiwara et al. (2011). But analysis on the coexistence space that such systems generate for every possible combination of competitive effects has not been explored. As a result, the hypothesis of coexistence in the parameter space being increased by ontogenetic niche shift has not been tested. Moll and Brown (2008) has proposed a very simple model to explain how coexistence could be possible in cases where inter-species competitive coefficients are greater than intra-specific ones (provided that this situation was restrained to only one life stage). An even more detailed model of the two-life-stages scenario is explored by Fujiwara et al. (2011), but in none of these cases has the extension to more life stages and the effect of ontogenetic niche shift on coexistence space been explored. In order to answer these questions, we propose a simplified version of Moll's model and we estimated the proportion of the hyper-dimensional parameter-space in which coexistence happens by using Monte Carlo techniques (Kroese et al., 2011) for a range of life-stage numbers.

The Model

The most basic version of the model is described by two competing species with two life stages each, with competition between the life stages of a single species assumed to be absent. Equally, competition between the life stages of two different species is also assumed to be absent. Similar cases can sensibly be assumed to happen in nature in several species (Werner and Hall, 1988; Werner and McPeck, 1994; Werner and Anholt, 1996; Arendt and Wilson, 1997). The lack of competition between species and stages is an assumption for the sake of keeping the model tractable. Such competition could of course exist in the real world, but is not relevant to the question being asked here. Figure 1 shows the basic diagram for a single-stage, two-stage and three-stage competition models.

The discrete time-step version of the system shown in Figure 1 can be expressed with the following system of equa-

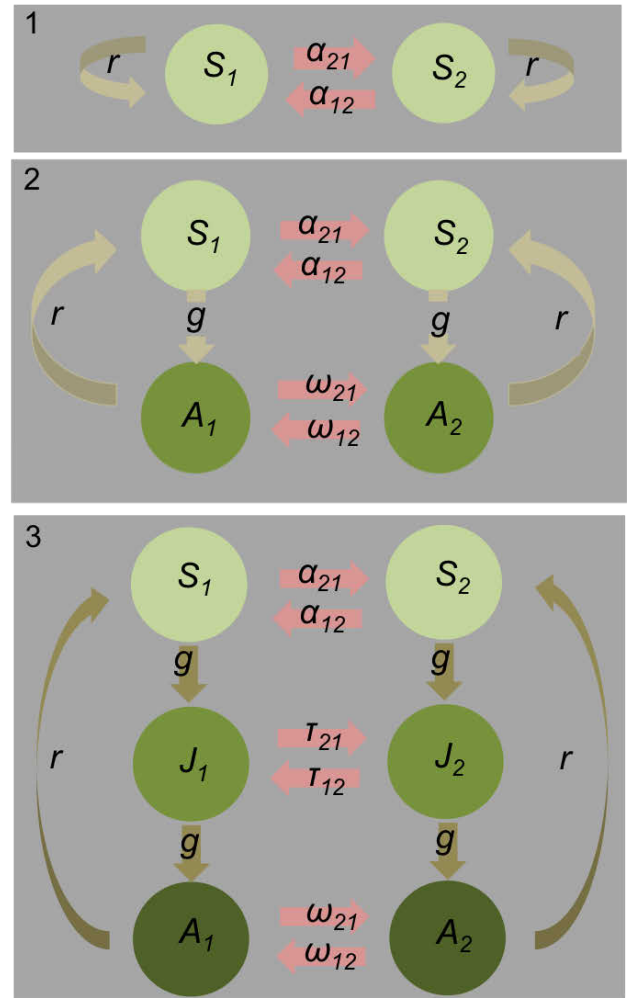


Figure 1: Diagrams for 1-stage, 2-stage and 3-stage models. Circles S and A represent the first and last stages respectively, J represents an intermediate stage between S and A , r is the adult reproductive rate and g is the individual growth rate, and competition coefficients are represented by red arrows between circles, (α , ω and τ). The model includes competitive effects in both directions and its values are standardized in relation to intra-specific competition. For instance, α_{ij} corresponds to the effect of species j on species i in the first stage of development.

tions for an objective species i . These are modified and extended versions of Moll's model (Moll and Brown, 2008) which is itself based on a two species Ricker (1954) model.

$$S_{i,t+1} = r_i A_{i,t} e^{-(A_{i,t} + \omega_{ij} A_{j,t})} + (1-g) S_{i,t} e^{-(S_{i,t} + \alpha_{ij} S_{j,t})} \quad (1)$$

$$J_{i,t+1} = g(p_{i,t})e^{-((p_{i,t})+\chi_{ij}(p_{j,t}))} + (1-g)J_{i,t}e^{-(J_{i,t}+\tau_{ij}J_{j,t})} \quad (2)$$

$$A_{i,t+1} = g(p_{i,t})e^{-((p_{i,t})+\chi_{ij}(p_{j,t}))} + A_{i,t}e^{-(A_{i,t}+\omega_{ij}A_{j,t})} \quad (3)$$

Where $S_{i,t}$ is the density of seeds of species i at time-step t , $A_{i,t}$ is the density of adults of species i and $J_{i,t}$ is the corresponding to middle stages; r_i is the rate of growth from adults to seeds, g_i is the growth rate between stages. α_{ij} is the competition effect of seeds of species j on species i , ω_{ij} is the equivalent for adults. The equation in the middle (Eq. 2) is the generic expression for any stage different from first or last; the value $p_{i,t}$ corresponds to the density of individuals in the previous stage for time t . Concordantly, the parameter χ_{ij} is a generic variable that corresponds to the competition coefficients in the previous stage. Intuitively it follows that τ_{ij} refers to the competitive coefficient of stage J . Extensions to more stages follow by incorporating new density parameters and competition coefficients. The effects on every life stage are calculated accordingly considering the proportion of individuals that stay at that stage and the proportion that move to the next one. These systems of equations are deterministic but analytic solutions can not be found (Hassell and Comins, 1976). It is possible to look for isoclines in the tetra-dimensional space of the 2-stage model, but since the interest is in investigating percentages of parameter space that converge on coexistence for many different number of stages, a simulation approach was selected. In order to explore this system some simplifications were done in relation to the original Moll and Brown model. The effects of differences in growth rate and reproduction rate between species are not considered. For this reason, reproduction rates and growth rates are fixed as the same for both species, in this case defined by g and r . The individual growth rate between stages within a species is also considered as the same: in other words, individuals develop at a constant speed. The model also assumes the intra-specific competition to be 1.0 and the top density for any stage (determined by the load capacity of the system) is also assumed to be 1.0 (see Moll and Brown, 2008, for more information). Scaling terms are not considered following the assumption that competitive coefficients are relative to intra-specific ones.

Methods

Model Dynamics

In order to follow the effect of competition coefficients on the dynamics of the model the values of r and g were fixed,

on $r = 1.5$ and $g = 0.5$ (unless specified differently). The argument for the selection of these values was based on a preliminary exploration and will be discussed later. The simulations were run for 150,000 iterations or until the system reached equilibrium. This number of iterations was selected after running simulations across the parameter space and noticing no important differences between increases in iterations from this value on. The result of a particular simulation was assumed to be coexistence if no species became extinct (density under 0.00001 on at least one stage). In cases where one of the species turned out to be excluded the identity of the species was recorded. Initial densities or quantities were selected randomly for all simulations. To explore the most basic 2-stage version of the model, four conditions were selected for the α_{ij} and α_{ji} values. In the first condition both alphas were set to 1.0, making the intra-specific competition the same as the inter-specific one for the first stage. In the second case alpha values were selected below 1.0, making the first stage a coexistence scenario. The third case sets one alpha as greater than 1.0 and the other as less than 1.0, making the initial stage a competitive exclusion scenario. Finally, the last case considers both alpha values as larger than 1.0, which in a single-stage scenario will create alternate states dependent on initial density conditions for the four quantities. On each of these conditions a full 2D landscape for ω_{ij} and ω_{ji} was explored. The range explored was between omega values of 0.0 and 2.0 with a resolution of 0.01; at each of these points 50 simulations were run starting from random initial quantities for S_i and A_i , creating 200 X 200 x 50 simulation plots as shown in Figure 2 in the results section. These results can be considered a replication of those obtained by Moll and Brown (2008). As shown by Wilbur (1996) and Moll and Brown (2008) the model exhibits a range of behaviours from stable equilibrium to chaos to oscillations. In this work the range of parameters selected does not show any other behavior except simple attractors. In this case the space of exploration for the competitive coefficients goes between 0.0 and 2.0. Individual growth rates g between 0.01 and 0.99 were explored, as well as adult intrinsic reproduction rates r between 0.95 and 2.5.

Exploring the 2-Stage Model

Each of the plots shown in Figure 2 could be interpreted as a slice of a tetra-dimensional space, where each dimension is characterized by the competition coefficients. On these slices the area of coexistence is a continuum square area that starts in the origin of the space (Moll and Brown, 2008, and Figure 2). With this knowledge, an estimation of the total hyper-volume of coexistence in the parameter space (from 0.0 to 2.0 on each dimension) could be obtained by estimating the omega values for which equilibrium coexistence stops being an attractor on both omega coefficients. In order to do this, one omega value is kept at 0.0 while the other explores simulations with values from 0.0 to 2.0 until coexis-

tence disappears. Once this has been done with both omega coefficients the proportion of the total coexistence area for that slice can be calculated by multiplying both omega values where coexistence does not happen any more, and then dividing this area over the 2.0 x 2.0 area of search. Doing this with every combination of alpha values creates a 3D landscape where each combination of alphas have an associated percentage of coexistence space in the omega slice. The total space can then be estimated by averaging all the percentages and in this way we can calculate an estimate that can be checked with the Monte Carlo simulation results that will be explained in the next section. This 3D landscape is shown in Figure 3.

Monte Carlo Simulations

In order to explore systems with more stages, a sensible way forward is taking random samples in the hyper-dimensional space and seeing in what proportions of these simulations coexistence is obtained. This approach is known as Monte Carlo search or ‘probing’. To do this, a large enough number of points should be selected to make a representative estimation. A set of tests were run using different numbers of points, and replicates. The conclusion was that 10,000 points and 10 replicates seemed to offer a good balance between small standard deviations and short simulation times. For each number of life stages between 1 and 10, Monte Carlo searches were performed (Figure 4). Also the effect of g and r values was tested and no qualitative differences were found.

Results

Results are divided in two parts: first an exhaustive exploration of the basic 2-stage 2-species model is explored (Figure 2 and Figure 3). Secondly the results for the Monte Carlo simulations will show the coexistence percentage of the parameter space for systems with different numbers of stages (Figure 4).

Coexistence in the 2-Stage 2-Species Model

The simple 2-stage 2-species model was explored for 4 different scenarios regarding the competitive coefficients of the first stage; a similar approach was followed in Moll’s work. In the first case (Figure 2.A) the competitive coefficients for the first stage, or alpha values, were set to $\alpha_{12} = 1.0$ and $\alpha_{21} = 1.0$. In this scenario the intra-specific and the inter-specific competitive coefficients for the first stage are exactly the same, which makes the system analogous to the 1-stage case, creating a 25% surface of coexistence for the omega slice. The second scenario (Figure 2.B) corresponds to the case where $\alpha_{12} = 0.75$ and $\alpha_{21} = 0.5$; these values were selected arbitrarily keeping in mind that they should be lower than one. Under this scenario the first stage suggests a coexistence case where inter-specific competition is lower than

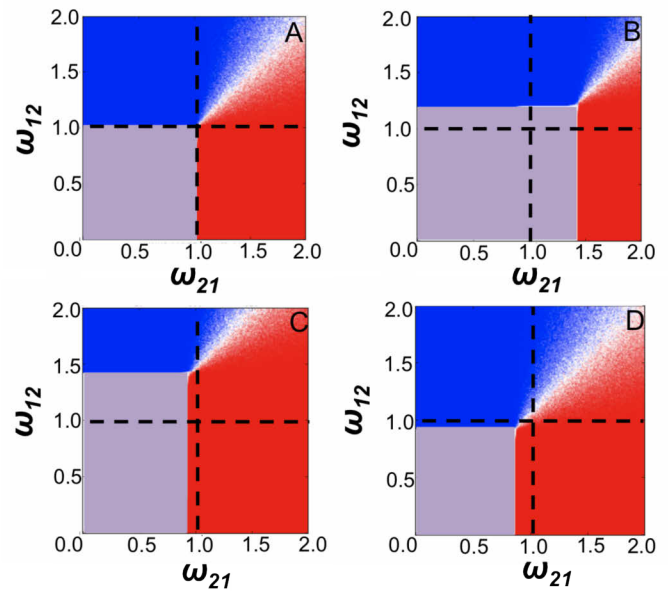


Figure 2: Results for combinations of ω values considering four different scenarios for α values. Values were explored from 0.0 to 2.0 with a step resolution of 0.01, creating 200 x 200 plots. Each point in this plot is the outcome of 50 simulations starting on random initial conditions for quantities S_i and A_i . For each simulation that species 1 won the point goes towards a red shift, for each simulation species 2 won the same happens towards blue. Coexistence is represented by purple, and in every instance is an attractor point (50 replicates converge to it). The figure shows how the coexistence region for the ω space can be expanded depending on the values of α . Plot A shows a case where competitive coefficients are equal to intra-specific ones, rendering the first stage ineffective in terms of outcome $\alpha_{12} = 1.0$, $\alpha_{21} = 1.0$. The B plot shows a case where both alpha values suggest coexistence, $\alpha_{12} = 0.75$, $\alpha_{21} = 0.5$. C shows the case where competitive exclusion would happen considering only the first stage $\alpha_{12} = 0.5$, $\alpha_{21} = 1.15$ and D shows the case where the initial stage would suggest an alternate state scenario $\alpha_{12} = 1.25$, $\alpha_{21} = 1.15$. $g = 0.5$, $r = 1.5$. Similar results can be found in Moll and Brown (2008).

the intra-specific. Such a case increases the area of coexistence when compared to the first scenario. Figure 2.C shows the omega space for the case $\alpha_{12} = 0.5$ and $\alpha_{21} = 1.15$; in this scenario the first stage suggests a competitive exclusion by species 1. In the space of possible second stage competitive coefficients this translates into a contraction of the coexistence space in the ω_{21} axis and an expansion in the ω_{12} axis, in relation to the first scenario. Finally, Figure 2.D shows the case where alpha values suggest alternate states dependent on initial conditions for the quantities S_i and A_i for every species i ; in this case the alpha values correspond

to $\alpha_{12} = 1.25$ and $\alpha = 1.15$ which creates a contraction in the coexistence area in relation to the first scenario.

Considering that the coexistence space remains as a continuous hyper-volume centred on the origin, a more exhaustive exploration of the space was performed. A plot that shows what percentage of the omega space (shown in the four scenarios of Figure 2) is composed by the coexistence region, per each combination of alpha values, was generated. Figure 3 shows such a plot, where the nonlinear nature of the coexistence space expansion for lower values of alpha justifies the increase in coexistence space in the 2-stage system compared to the 1-stage version. The implications of this, and its relation to further results in Figure 4, will be discussed below.

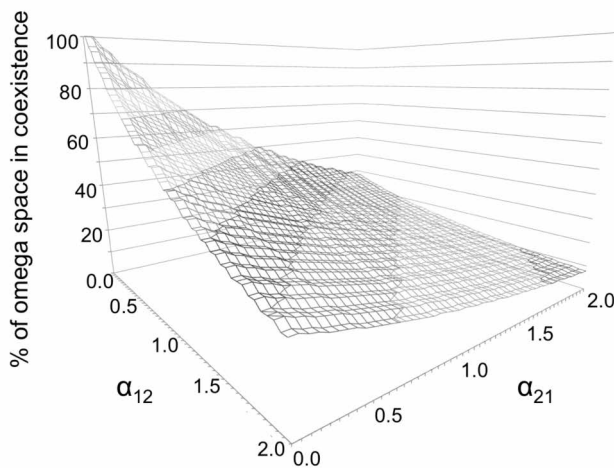


Figure 3: The figure shows the alpha space, where every combination of alpha has an estimated percentage of coexistence area in the omega space (Figure 2). The figure shows the non-linearity in the growth of the coexistence space for low alpha values. This in turn shows that the magnitude in cases where the coexistence area expands in relation to the 1-stage model (25% coexistence) is greater than the contraction in other cases. $g = 0.5$ $r = 1.5$

More Than Two Stages

Monte Carlo simulations for a range of multiple stage systems (from 1 stage to 10 stages) were run and the results are shown in figure 4; each bar represents the average value of 10 Monte Carlo runs with 10,000 random points in the entire parameter space; initial conditions for density quantities are randomly selected. Error bars, both positive and negative, represent a single standard deviation from the average. The decrease in coexistence space after 3 stages is due to the averaging effect of systems with many stages and it will be

discussed and explained in the next section. Dimensionality of the parameter space increases with stages but the number of points considered in the Monte Carlo simulations is enough for the standard deviations not to grow beyond sensible ranges.

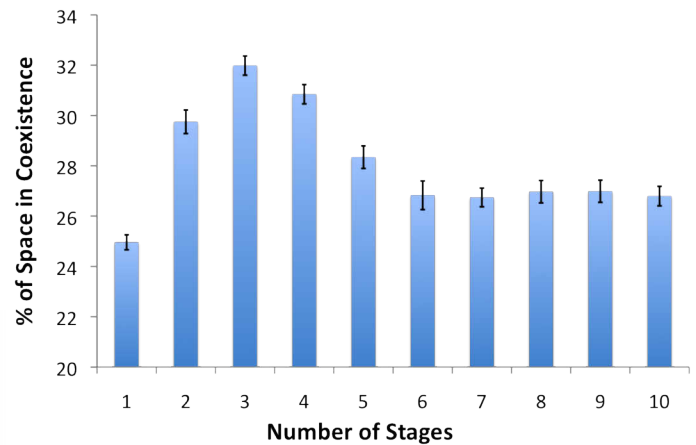


Figure 4: Percentages of the hyper-dimensional parameter space for competition coefficients that converges to coexistence. Results obtained by 10 replicates of 10,000 point Monte Carlo searches. The error bars correspond to a single standard deviation. The proportion of the parameter space that converges to coexistence seems to be increased around a 3-stage scenario and then drop down when more stages are added. $g = 0.5$, $r = 1.5$.

Discussion

Ontogenetic niche shift is a well-documented process that produces a niche separation, and in some cases isolation, of different developmental stages in an organism's life. Previous theoretical work has shown that such processes can be interpreted as an adaptation that arises from the reduced intra-specific competition and associated fitness gain for individuals that exhibit some degree of separation between life-stage niches (Claessen and Dieckmann, 2002). In nature, cases of ontogenetic niche differences are abundant in plants, insects, amphibians, and fish. These cases offer a very clear picture of what it means to have two separate life stages with different niches. For instance, adult frogs and tadpoles live in different ecological niches, predated different sources of food, and being predated by different trophic levels. Similar cases can be seen in numerous species of fish that, during their development, move to different trophic levels and as a result to different ecological niches within the ecosystem (Werner and Hall, 1988). In the case of plants, which are of particular interest in coexistence research, different life stages can also be present. For instance, the environmental constraints and challenges during germination and plantule stages could be very different to the ones

present as fully grown adult plants (Eriksson, 2002). Although these scenarios strike us as obvious cases of ontogenetic niche shift, it seems hard to argue that coexistence of a large number of species in big communities (such as tropical forests or plankton communities) happens due to the effect of this characteristic on every single species evaluated. With respect to this point it is important to point out that such stages might not need to be obvious in the morphological sense for them to be functionally present. Certain ecological dynamics in terms of prey size (Mittelbach et al., 1988) and locomotion ability (Padisák et al., 2003) can happen with very small variations in phenotypic characters. In the same way, light capture and soil dependence could shift suddenly between different plant niches (Auffret et al., 2010). In other words, the presence of morphologically obvious differences between stages is an indication, but not a condition, for having different ecologically functional stages during development. Because the values for competition coefficients are relative to the intra-specific competition for that stage, and similarly individual growth and adult per capita reproductive rates are also relative to these values, similar results can be obtained with different competition coefficients and values for g and r .

The 3 Stages Bump Explained

The most interesting result shown here is the increase in the size of the coexistence region that exists in the parameter space systems with 2, 3 and 4 stages. After this increase the coexistence region seems to shrink again when more stages are added (Figure 4). In this pattern there seems to be two different effects at work. First, the addition of more stages seems to increase the proportion of space that corresponds to coexistence; this is shown by the results in Figure 3, where the nonlinear increase of coexistence space for low alpha values is bigger than the contraction for bigger ones, as in the case shown in Figure 2.D. Following this example it would be intuitive to assume that more stages allow for more coexistence; in a biological sense this translates to more scenarios where good outcomes in certain stages can maintain a species' survival despite bad outcomes in other stages. The drop in coexistence when adding more than three stages comes about because of a counteracting trend that happens when selecting random values for the competition coefficients. In order to understand the problem in an intuitive way, consider that every multi-stage system can be equivalent to a 2-stage case with different growth and reproduction rates. In Figure 5 a diagram explaining how to build an analogous 2-stage model from a multi-stage one shows how the randomly selected competition coefficients for the first stages tend to average around 1.0 for sampling between 0.0 and 2.0. This creates an analogous model where the first-stage competition is neutral to the outcome of the dynamics. In this way the incorporation of more stages approximates the model to the one described in Figure 2.A, where the

coexistence volume is close to 25%. This result is not an artifact in the sense that the Monte Carlo simulation is not biased in any way; the parameter space “eats” itself when more dimensions are added.

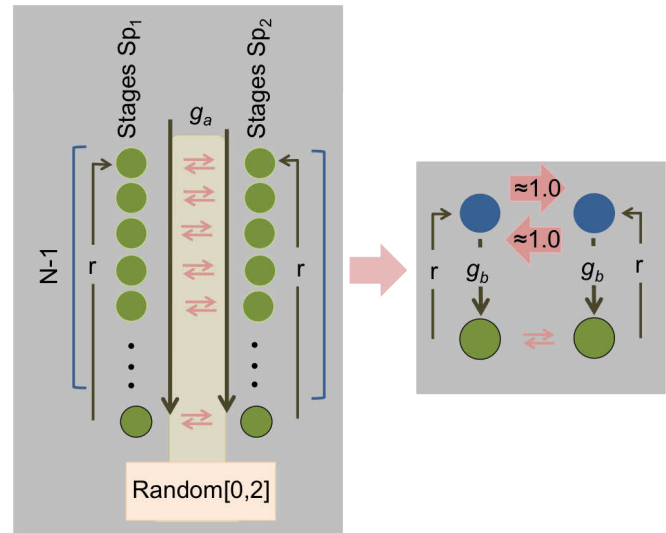


Figure 5: The detrimental effect of multi-stage systems on coexistence considering a system with N stages (left side); the random search for competitive coefficients in the space $[0,2]$ will converge to a scenario where the inter-specific competition for the first $N-1$ stages are analogous to a single stage with values close to 1. As shown in Figure 2.A this case represents a similar proportion to the single stage case, with only 25% of the space converging to coexistence. The only difference would be that in the analogous case the individual growth rate will be reduced due to the compression caused by merging $N-1$ stages ($g_a > g_b$), but this would not have an impact on single stage models.

Another way to understand this outcome is by considering the hypothetical case where the number of stages is infinite; in this case we would be looking at a continuous life development where competition only happens between same-age individuals. That scenario could also be analogous to noisy competitive abilities during development. In any of these two interpretations the effects of the two-stage niche segregation are lost, and the competitive coefficients can be averaged and considered as a single stage model, with 25% coexistence space in the range $[0,2]$ for competitive coefficients. In nature, it can be sensibly assumed that over long periods of time the competition coefficient from the point of view of an objective species in relation to every competitor in a particular niche can vary. This would thereby create a pseudo-random sampling of competitive coefficients for every stage, over evolutionary timescales. It is tempting to state that under this consideration, the apparent presence of no-more-than-3 stages in most species with obvious ontoge-

netic niche shifts could be assumed as an adaptation for individuals of species that experience long term fluctuations of competitors in their different developmental niches. In order to test this hypothesis further work needs to be done, specifically taking into consideration the effects of reduction of intra-specific competition and co-evolutionary dynamics in multiple-species scenarios. Nevertheless, the results shown here suggest that such an idea could have the potential to explain such a trend in nature.

Competition Between Stages

After a quick review of the results it might be apparent that this model relies heavily on the niche isolation between life-stages, which translates into diminished or absent vertical competition between stages. The effects of the inclusion of vertical competition will affect the results observed here depending on the magnitude considered. Hypothetically an equivalent scenario can be obtained if g and r rates are increased in certain stage transitions relative to others. The incorporation of vertical competition coefficients could show potential to explore a continuous spectrum with different degrees of isolation between stages. The expected result of such a model would be that at one end of the spectrum, where the impact of vertical (and diagonal) competition is fully considered, the model will converge back to the 1-stage scenario considering the competitive coefficient values as a function of all the coefficients involved. At the other end of the spectrum the effect uncovered by our model would be observed.

More Than Two Species

In this work the considerations regarding competitive intransitivity between species were not analyzed. Nevertheless, the model proposed can be considered, in a simplified scenario, as a multiple-species case for any objective species i . Under this interpretation the effect of the second species can be said to be the weighted effects of all the species present in a particular niche. This is just an interpretation of the model, but in terms of the dynamics it does not capture the full effect of the competitive relations between species. Further work should be done in order to accommodate these cases.

Natural Selection as a Promoter of Biodiversity

As a final point of discussion, it is important to consider in parallel the implications of: a) the results obtained in this work and b) the nature of ontogenetic niche shifting as an adaptation. As shown by Claessen and Dieckmann (2002) ontogenetic niche shifting can be seen as an individual adaptation responding to a pressure to reduced intra-specific competition. At the same time, ontogenetic niche shifting can potentially be seen as an adaptation to reduced inter-specific competition for objective species in changing environments. Such conclusions lead to a scenario where a process driven by natural selection at one scale promotes

coexistence and by extension biodiversity at another scale. Usually, natural selection has been seen as a process that reduces diversity in classic evolutionary theory. A further analysis of processes like the ones discussed here could show that under certain conditions natural selection can actually provide the basis for biodiversity rather than constrain it. Further analysis and model development to test this idea should be considered, but the result shown here seems to indicate that this could be the case.

Conclusions

A review and classification of the current competition models that explain species coexistence framed the multiple life-history-stage version as a trade-off model. It was shown that such a model increases the percentage of the parameter space that converges to coexistence equilibrium points in cases with two, three and four stages. The effect is diminished by the incorporation of more than four stages due to the averaging effect of randomly occurring competitive coefficients, which effectively reduce the model to a single-stage case. The innovation of this piece of work relies on the approximation used to evaluate the coexistence space and the discovery of a non-linear pattern between the proportion of coexistence space and the number of stages. A set of more evolutionarily oriented simulations should be explored to determine the soundness of an adaptive explanation for biological species having no more than a particular number of life stages.

Acknowledgements

This work was supported by an EPSRC Doctoral Training Centre grant EP/G03690X/1.

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