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Species Coexistence in Spatial, Non-Equilibrium Environments

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Species Coexistence in Spatial, Non-Equilibrium Environments

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Pierre Churukian

Committee in charge:

Professor Stuart A. Sandin, Chair
Professor Brice X. Semmens
Professor Jennifer E. Smith

2019

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University of California San Diego

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ABSTRACT OF THE THESIS

Species Coexistence in Spatial, Non-Equilibrium Environments

by

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A challenge in ecology is to understand how so many species are organized in their communities and which coexistence mechanisms act to maintain diversity. The methods of ecological theory can further challenge by incorporating implicit assumptions. The non-equilibrium approach is useful as it includes the fluctuating environments so prevalent in nature. A growing number of empirical works attempt to quantify coexistence mechanisms. Recent developments in Modern Coexistence Theory in combination with tools from Spatial Simulation can leverage long-term field observations as well as the experience of field ecologists to create spatial models for use as a hypotheses-testing platform. An individual-based model of community dynamics is presented using a framework of Pattern-Oriented Modeling to serve as validation.

1. Diversity Maintenance

Why do some systems have so many species with similar ecology? This is not a new question, Hutchinson (1959) asked the same in the subtitle of a seminal paper "Why are there so many kinds of animals?". Based on classical ecological thought, we can ask why the superior competitor hasn’t dominated and excluded all others? Or if the diversity far exceeds the resources, we can ask how the communities might be organized to support this diversity?

These questions are difficult to answer directly, especially with long-lived organisms operating on long time scales in open systems, where dispersal and migration are important. Attempts have included an assortment of ecological tools, from (a) experimental manipulations to (b) trait – phylogeny – environment relationships and (c) demographic analysis of frequency-dependent rates. Theory is an additional tool at our disposal, wherein rigor is used to extend our intuition, develop new methods and interpret results. However, theoretical ecology has offered little of utility to field ecologists and naturalists who are not able to match their observations to the predictions of theory However, recent theoretical developments (Chesson, 2008; Ellner at al., 2018) have yielded promising tools allowing, in particular, the analysis of partitioning of temporally varying resources.

Theory describes some ecosystems well, particularly the model systems often used by ecologists but also the managed ecosystems that get most concern, for example parks, forestry areas and farms. This allows prediction of outcomes with some accuracy and allows for the interpretation of collected data for management decisions. However, there are some highly diverse systems are not well-described by theory. In particular, coral reefs and tropical rain forests are the commonly cited examples (Connell, 1978). In reality, most naturalists and field ecologists find little need for the predictions of ecological theory, except citing it to serve as a solid foundation to contextualize their work, which is often at the level of individuals and bears little resemblance to the hypothetical communities of ecological theory. This is understandable, even among theoretical ecologists, the expectation to find general laws is waning. Early on, MacArthur (1972) suggested the goal was to find general rules, but the claim starts to change, McIntosh (1985) claimed, “Ecology was not and is not a predictive science”, Lawton (1999) called community ecology “a mess” for finding general rules, Simberloff (2004) went as far as to say that the complex nature of communities actually precludes general rules. Most of all, the experience of naturalists and field ecologists was not confirming the theories and workers were finding no use for the theoretical tools offered.

Demographic and Autecological Paradigms

It is hard to overstate the role of paradigms in ecology. Kuhn (1962) warns how all observations are "theory-laden" and influenced by the underlying paradigm, often implicitly. He also asserts that paradigms are mutually exclusive, so the adoption of one implies the exclusion of all others. Thus it is surprising to see the concurrent operation of two paradigms in ecology, raising the question why one has not yet expired. The older, still-prevailing paradigm, named the *demographic paradigm*, postulates a form of numerical control which Darwin (1859) codified for biological processes having brought together economic ideas of Adam Smith, Malthus and others from physiocratic Europe (Hengeveld & Walter, 1999). This gave rise to an ecological framework where competition is seen as a structuring force (Fisher, 1930; Gause, 1934), and eventually given law-like status in the Competitive Exclusion Principle (Hardin, 1960). The ecological framework also neglects spatial and abiotic processes, as remarked by a noted biologist, "Ecology is non-dimensional, at scale of the local naturalist" (Mayr, 1954). From this framework, theoretical statements were being put forward, for example the concept of *limiting similarity*, that organisms must be different in order to coexist (Hutchinson, 1959), (MacArthur & Levins, 1967). The appeal of these statements is in their intuitiveness, by conforming to the expectation of naturalists and field ecologists for some cases, many are encouraged to expect generality from these statements. This particular statement has borne out (Chesson, 2000), however, given need to eliminate the messiness of the natural world in order to apply the tools of demography, it comes as no surprise that predictions made from this ecological framework were realized only in a small subset of cases. “Scientists have made fun of Middle Age scholars discussing the number of angels that could dance on a tip of a pin. For many years, modern ecologists have made whole ecosystems dance the same way, thanks to the mathematical models of Lotka and Volterra.” (Margalef, 1997).

The demographic paradigm emphasizes organisms embedded in stationary local populations contained in a local community. Within populations, species are only considered for resource utilization and biotic processes that feed back on system. Within communities, species are considered for trophic level and status. Entire ranges of variation are reduced to summary averages and individuals' behavior is imposed by higher-level constraints, for example, lack of resource. These ideas can be formalized as Classical Competition Theory which grew from the Hutchinson (1959) argument, the essential assumptions of which are:

- (1) Life history characteristics can be summarized by per capita growth rate.
- (2) Deterministic equations can model population growth; in particular, environmental fluctuations can be ignored.
- (3) The environment is spatially homogeneous and migration is unimportant.
- (4) Competition is the only important biological interaction.
- (5) Coexistence requires a stable equilibrium point (Chesson & Case, 1986).

In many ways, this does provide a useful approximation and allows formulation of models which show mechanisms of coexistence familiar to naturalists and field ecologists, for example, direct interaction, resource partitioning, frequency-dependent mortality. However, the inherent limitations must be acknowledged and accommodated.

Scaling up to community ecology within the demographic paradigm, attention has been on general models built from population dynamics of pairs of species and relying on the concept of a community matrix to scale pairwise relationships to the community level. Generally, performance is measured by population growth and models attempt to replicate the deterministic outcomes of local interactions between functionally distinct species and their environments (Hengeveld & Walter, 1999). Communities are seen as a combination of the component populations’ dynamics and the cradle of the optimization processes and the equilibrial levels, a notion dating to Darwin (1859). Of particular importance, is the assumption of equilibrium. In this approach, systems are seen as usually at equilibrium, and exclusion is the result of disturbance, as in a successional sequence. Communities exhibit a “balance of nature”, thus are predictable and directional (Cooper, 2001). Linneaus (1707-78) considered nature to be in equilibrium. Adam Smith (1723-90) gave idea that competition leads to equilibrium. Hutchinson (1948) assumed equilibrium evident in “self correcting mechanisms". As a fundamental assumption of classical competition theory, the assumption that competition is of overriding importance becomes central to equilibrium ecology. This distinction between equilibrium and non-equilibrium ecology is not commonly noted, but has been characterized by Chesson and Case (1986) and elaborated on by Rohde (2005).

In contrast, there is a concurrent, competing paradigm, the so-called *autecological paradigm*. It emphasizes how individual organisms cope with a nonstationary environment that is temporally and spatially heterogeneous. “Individual organisms are insular in their grappling with life; their environment is unknown to them from one moment to the next, and from one site to the other. They are adrift without any holdfast or prospect, they can rely only on their adaptive characters to get them through” (Walter & Hengeveld, 1999). Resources are only one of many ecologically significant aspects. Biotic processes are only secondary modifiers of the patterns set by the organism-environment interaction. It is much less developed than the demographic paradigm, but a number of workers have furthered the approach. Notable examples are the Dynamic Energy Budget models (Kooijman, 2010) and the Metabolic Theory of Ecology (Brown et al., 2004).

Complex Adaptive Systems

Most ecologists can agree that nature is complex, and how this complexity should be treated by ecological methods is an important theoretical question, in particular as traditional methods use simplifying assumptions that possibly invalidate the efforts. Alternatively formulating the questions in the language of complex adaptive systems can prove useful. In particular, it avoids the simplifications of artificiality of closure or presumption of equilibrium, but these non-parsimonious models then raise new philosophic questions. Taking from the experience of urban development, Batty and Torrens (2005) illustrate these questions with the evolution of models in their field to handle complexity. Many of the questions to contend with are ontological, i.e. do we expect irrefutable answers?, but some are epistemological, i.e. do we believe the model can show something meaningful?, and these question the validity of our findings as the difficulty of testing each causal chain in non-parsimonious models can result in actually not testing the implicit causal structures, relying on approval from stake holders, and ultimately plausibility being taken as evidence.

A systematic means to conduct hypothesis testing and theory development is not necessary for urban development as it is for ecological studies, so we reformulate the method as follows. Considering ecological communities as complex systems, i.e. "an entity, coherent in some recognizable way but whose elements, interactions, and dynamics generate structures and admit surprise and novelty that cannot be defined a priori", (Batty & Torrens, 2005), allows the use of simulation as a “virtual laboratory” for exploring those structures in state space configurations untenable in nature. This was done as purely abstract rule-based systems (Wolfram, 2001) and found only limited purchase in ecology (Molofsky & Bever, 2004) (Kalmykov & Kalmykov 2016). Avoiding the purely abstract, more promising work has gone into the individual-based modeling and ecology (Grimm & Railsback, 2005; Breckling et al., 2006) which insists on modeling the individuals as fitness-seeking and adaptive. This is in contrast to the reductionist approach of excessive simplifying assumptions with time modeled away with equilibrium, and spatial and abiotic processes neglected. The cost of these simplifications may not be immediately apparent, but recalling how little relevance most ecologists see in theory, we can ask, “What good is a simple model of a complex system?” (Webb, 1996).

2. Coexistence

Equilibrium Vs Non-Equilibrium Definitions

Coexistence can be defined precisely, but here again, the paradigms affect the definitions. All in cases, coexistence is not transient, none of the species will ever reach extinction, and we say species are *co-occurring* if not coexisting (sometimes called unstable coexistence). They could be stochastically walking to extinction by neutral dynamics, slowly being driven extinct by others in the assemblage, or maintained in a local area by dispersal from other areas (Chesson, 2000).

Equilibrium systems base the definition of coexistence on the definition of population regulation, which is when a population displays properties of persistence, boundedness and a return tendency. The current view (Hixon, Pacala & Sandin, 2002) is that (1) population regulation is caused by demographic density dependence. (2) Density dependence is necessary but not sufficient for population regulation. (3) Both competition and predation are possible sources of density dependence. This is then extrapolated to the community level and as such, community-level coexistence is seen as an approach to a long-term trend, characterized by (1) conservation: little tendency to lose species with time; (2) recovery: from events that drive any of the species to low density; (3) assembly: can be built up by immigration of species from outside the system; (4) irrelevance of history: approaching equilibrium, effects of past abundances disappear (Chesson & Case, 1986).

Non-equilibrium systems characterize coexistence by persistence, rather than constant abundances. They are characterized by mechanisms of coexistence which are fluctuation-dependent and species densities do not remain constant over time in each spatial location (Chesson & Case, 1986). Commonly non-equilibrium in populations refers to where local populations do not trend towards a point equilibrium, for example density-vagueness of Strong (1984) or stochastic boundedness of Chesson (1978), but these are still essentially non-spatial systems. Species in non-equilibrium scenarios can be co-occurring, with no tendency for recovery and species are not maintained in system on long timescales, or coexisting, where densities of species in the system do not show long-term trends. If they get low, they tend to recover. The same properties define a stable community for both equilibrium and non-equilibrium theories, but here the invasibility criterion is the test for coexistence, that each species can increase from low density in presence of the resident community. A key quantity is the long-term low-density growth rate, or *recovery rate*, if positive, the invader increases from low density. For a species to have a positive recovery rate, it must be distinguished from other species in ecologically significant ways. It confirms concept of limiting similarity in contrast to unified theory which asserts species equivalence. This is still a “balance of nature”, but defined by regulation instead of equilibrium (Cooper, 2001), as only randomly walking populations are unambiguously nonequilibrial, all other usages are misplaced (Cappucino, 1995). Relative to the equilibrium approach, this brings important changes to the ecological framework. Firstly the focus on environmental fluctuations, but, importantly, competition is no longer seen as the only important biological interaction, this allows for a much broader range of ecological phenomena to be considered.

Modern Coexistence Theory

Modern Coexistence Theory (Chesson & Warner; 1981; Chesson, 1994; Chesson, 2000; Chesson, 2003) provides a framework to examine mechanisms of maintenance of species diversity, they include fluctuating conditions unsuitable to other methods. The basis of the approach of Modern Coexistence Theory is to decompose the quantities of interest and compare the parts. So the recovery rates, the key metric, are decomposed into a sum of different effects, elucidating underlying processes. In particular, decomposing into resident and invader rates is useful since, by definition, a mechanism stabilizes coexistence of species A and species B if it gives each, when it is rare, an advantage over the other. To have this, the mechanism can help the rare species, or it can hurt the common species (Ellner et al., 2018).

Consider an experiment with two species coexisting in a tank, ito ask if the coexistence is due to variation in the temperature. It might occur to us to do a simulation or experiment with the temperature held constant, however, this can strongly affect the community structure and so the result of such an experiment would be confounded by the effects of the changes to the competitive interactions, the age structure and other changes. Instead, the invader–resident comparison is evaluated in a single experiment when all processes are operating, and terms involving the variance can be collected using the methods of Modern Coexistence Theory to quantify the direct effect of variance in temperature (Ellner et al., 2018).

In addition, by separating on a shorter and longer time scale, given that focus is on mechanisms operating on the longer time scale, Chesson (2000) has shown that recovery rates can be partitioned into two types of mechanisms, mechanisms relying on equilibrium and on the shorter time scale, and mechanisms that rely on the fluctuations of the longer time scale. It is the isolation of these fluctuation-dependent mechanisms that makes the technique so powerful. This yields an expression as $r_i = \overline{r_i} + \Delta N + \Delta I$ which demonstrates such a partition. The ecological interpretation of these partition is an active area of research, however it does provide reassurance of the comprehensive of the partition. These three mechanisms in particular have been termed fluctuation-independent effects, relative nonlinearity and the storage effect, respectively.

The term ΔI is the *storage effect* and represents the contribution to the recovery rate from the temporal partitioning of resources and depends on responses of the species jointly to the temporally varying physical environment and temporally varying competition.

Using these concepts, storage effect theory derives the conditions under which climate variability will have stabilizing or destabilizing effects on species coexistence. Consider a set of fluctuating populations that maintain their local diversity without input from immigration. If some years favor one species, and other years other species, then from models of simple systems of this sort (Chesson & Warner, 1981), we can expect the interaction to be stabilized (ie, local community recovers from extreme perturbations, without immigration). This is the first condition, (1) species must differ in their response to climate variation, the result of which is the species experiencing relatively more intraspecific competition during its favorable years and more interspecific competition during its unfavorable years. Two more conditions are required for coexistence by this mechanism, (2) species must have long lifespans to buffer their populations against unfavorable years, otherwise gains made in the favorable periods will be immediately lost during a bad period. Finally, (3) the competitive impact on each species must be increased in favorable years relative to than in unfavorable years (Adler, 2006). The third item is the *density-dependent covariance* between environment and competition by which we will test the storage effect (Ellner, Synder & Adler, 2016).

The condition (2) of buffering depends on subadditivity in the response of growth rates to environment and competition. This is an interaction between the environment (which influences ecological rates) and competition, in the way they affect the growth rate of a population as shown in Figure 1. If growth rates are subadditive, then, as the quality of the environment decreases, the decline of growth rate with increased competition becomes less steep, in which case, there is a buffering effect (Adler, 2006). This means there are times a species experiences a good environment and gains the performance benefit without the losses of high competition. Conversely, species that experience a bad environment may maintain positive growth in spite of any surrounding competition. While this may sound abstract, there are numerous ecological examples, including long-lived adults, dormant life stages, seed banks, long-lived egg sacks, or diapause. Consider a seed bank, even if a bad environment for reproduction occurs, the germination rate can never fall below the level of the seed bank, as this is independent of seed production, thus acting as a buffer, leading to interactive effects of environment and competition.

The condition (3) indicates a positive covariance between the environmental

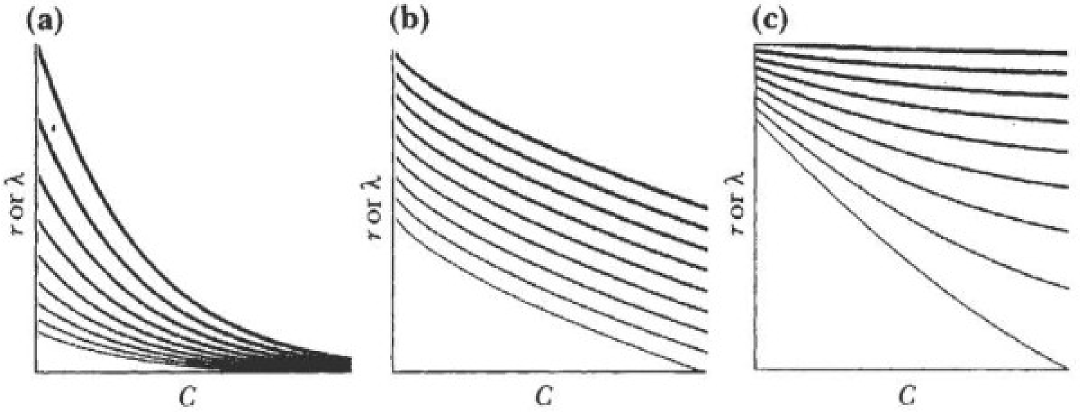


Figure 1: Interactions between environment and competition in their determination of population growth rates. Within each panel, each curve represents a different value of the environmental response, with thick lines indicating more favorable environments. (a) Buffered growth, (b) Additive growth (c) Positive interaction. (Chesson, 2008)

dependent parameters and the competition. For example, when a species has intense recruitment, it may result in more competition for space among recruits. Environmental fluctuations that affect recruitment will then carry over to fluctuations in competition. Recall that where correlations consider the closeness of relationships, covariance considers the magnitude of relationships. It is reasonable to expect the competitive response to depend on the environmental response, or least be correlated with it. Note the competitive response of a species depends on environmental responses of all the species in the community. At high density, species tends to have positive covariance. At low density, covariance weakens or becomes negative, so species have more variation in conditions.

Figure 2 puts this all together in an illustrative diagram. The points show population growth when the covariance affects the resident more than the invader. When the resident has a good year, it experiences high competition, so the resident has only moderately good population growth. In contrast, when the invader has a good year, it experiences low

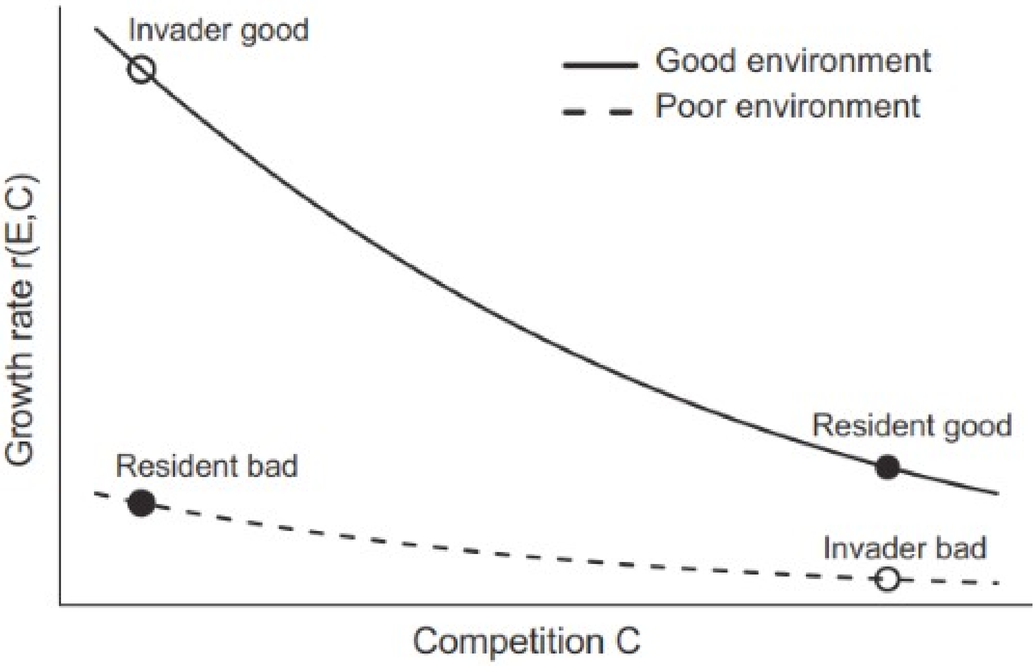


Figure 2: Environment-competition covariance and subadditivity can produce the storage effect. (Ellner, Synder & Adler, 2016)

competition (because the invader is rare, and the resident is either having a bad year or does not compete much with the invader), so the invader has high population growth. Because of subadditivity, the invader's gains in good years are much greater than losses suffered in bad years (Ellner, Synder & Adler, 2016).

The second fluctuation-dependent mechanism, *relative nonlinearity*, has been less studied but can also be a significant contribution to species coexistence (Yuan & Chesson, 2015). Relatively nonlinear growth rates can arise simply from differences in life history traits, many kinds of temporal variability can then interact with these nonlinearity differences to give a contribution to coexistence. In some circumstances relative nonlinearity is stronger than the storage effect or is even the sole mechanism of coexistence. In this case, different species must have different nonlinear responses to competition as in Figure 3. If competition fluctuates over time, then Jensen's inequality means that the long-term growth rates, which are time averages of short-term growth rates, will be affected differently for different species. This promotes coexistence when species drive fluctuations in competition in directions that favor their competitors. The coexistence mechanism thus involves both the relatively nonlinear growth rates and differences between species in their contributions to fluctuations in competition.

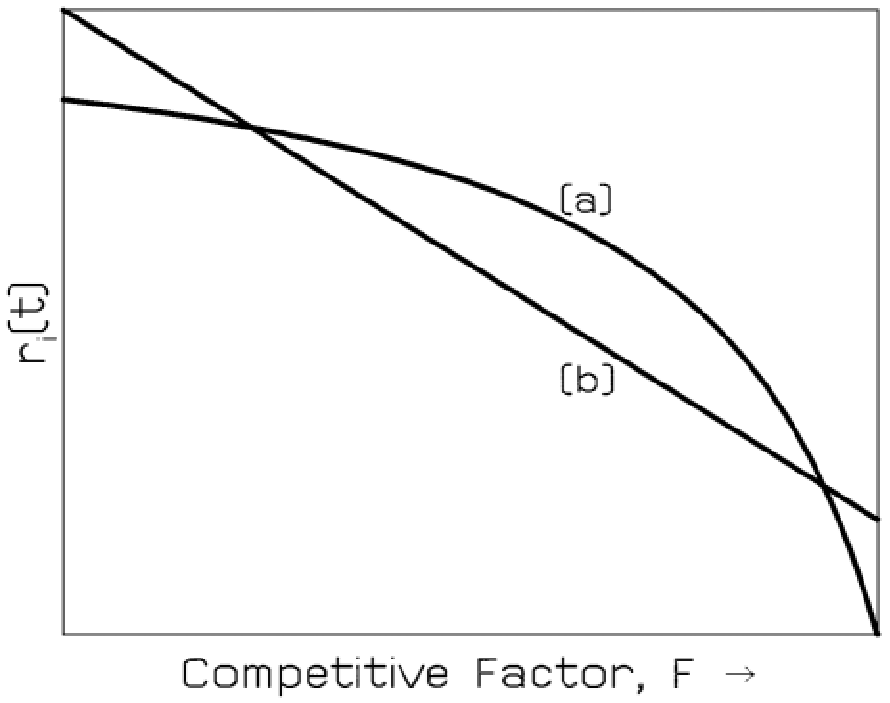


Figure 3: Relative nonlinearity of growth rates.

Consider a community with three species each with its own community interactions. To ask if these species are maintained by some coexistence mechanism, we use *invasibility analysis* to determine if the invasibility criterion is satisfied. To evaluate invasibility of one species, call it A, it is removed from the community; the resulting community with residents B and C is allowed grow until a stationary distribution is reached, A is reintroduced at low abundance (called the invader) to verify that it can consistently increase in abundance under these conditions. The process is then repeated for species B and C as invaders. Stable coexistence requires recovery of populations from low density without immigration thus recovery rates are a key metric. (Chesson, 2008)

3. Applications

Since not all species differences will contribute to coexistence, but only those that lead to differential success in the various density-dependent processes that regulate their abundances will promote coexistence, and thus foster the invasibility of each species. In their survey, (Siepielski & McPeek, 2010) noted the tendency of ecologists to assume organisms found together in the field were coexisting, out of 323 of empirical studies of multiple species living sympatrically, only seven tested invasibility. Relevant empirical application investigating coexistence tend to rely on either long-term datasets combined with statistical modeling or on model systems with short generation times and convenient logistics.

Analytically derived models

Studies based on fitting data to analytically-derived models, as set out in Chesson's original work, are complicated by the need to derive a new model for every system being studied. Sears and Chesson (2007) used neighbor removal experiments to study a component of population growth rate, comparing the contributions of a storage effect and local competition to seed production in two desert annuals. Angert et al. (2009) worked with a desert winter annual plant community, investigating a trade-off between relative growth rate and resource use efficiency to show population dynamics consistent with recovery from low density. Using an long-term dataset from permanent quadrats, an analytic model was derived to get estimates of germination, survival and fecundity, which were then partitioned and analyzed statistically. These analytical model, while powerful and successful, tend to obscure the elegance and power of the underlying ideas. Even

Chesson himself proposed (2008) a combined experimental and modeling approach for assessing coexistence.

Simulation-based models

A further development is seen in a series of studies based on using data from simulation or observation to supplement the analytical aspects. Here parameters are estimated from a dataset and various scenarios are simulated using those parameters to generate metrics. By doing so, the need for a case-specific model is avoided, as is the need to make a small variance assumption necessary for the analytical models. In addition, this approach has the flexibility to partition coexistence in terms of different mechanisms than the mechanisms used in Chesson's original work.

Examples include Adler et al. (2006) which used over 30 years of observational data in a prairie community of perennials to show interannual variation in plant performance in relation to varying climatic variables, which increased recovery rates, and thus coexistence. Adler, Ellner and Levine (2010) brought some creative ideas leveraging multiple models and parameter sets. By using two models, one spatially explicit and the other spatially implicit, the contrast between them gave insight as did the ability to set various parameters to zero so as to simulate the absence of a process. This approach to using modeling as a "virtual laboratory" in which to run experiments difficult to do otherwise can be seen as a way around the limitations of Modern Coexistence Theory. Ellner, Snyder and Adler (2016) went some ways in developing the technique of using a general Monte Carlo simulation in place of the analytic system-specific small variance approximation. The central idea is to compute each growth rate twice for each species, by simulating the model with and without environment-competition covariance. Ellner et al. (2018) extended the techniques to further mechanisms and attempts to recast the theory as less analytical and more suited to empirical or applied work.

Laboratory Systems

Studies based on laboratory investigations of short-lived organisms include Descamps-Julien and Gonzalez (2005), Gliwicz and Wrzosek (2008), Jiang and Morin (2007) and Stomp et al. (2004). The pragmatic aspects of laboratory work and the clarity of results are offsets by the limited selection of systems suitable for a laboratory.

4. Modeling

Methodology

Observations of field ecologists are at level of the individuals, and it is interaction and behavior at this level that leads to emergence of patterns at larger scales. The stylized nature of the demographic paradigm leads us to tools that ignore aspects of life history which are essential to system. This limits our ability to relate pattern to process or even to interpret observations made. On other hand, the tools afforded by the autecological paradigm are much better suited to studying communities. One key feature is to base the description of individuals' behavior and interactions on first principles rooted in energetic or evolutionary theory. (Grimm & Berger, 2016). Spatial simulation, a spatially explicit, bottom-up modeling approach that includes individual-based models and cellular automata. Where the demographic methods treat spatial heterogeneity and individual variation as noise, these are seen as central to the autecological paradigm. In addition the commonly used modes of computing favor the iteration and heuristics of spatial simulation, in particular the possibility of algorithmic solutions is very promising (Wallentin, 2017).

On the other hand, there are limitations to the method that must be accommodated. Firstly, the lack of rigorous mathematical structures leaves the burden of proof unmitigated and so the researcher must find alternative, often creative, ways of establishing validity. Secondly, the rule-based approach utilized has drawbacks in regard to their specification as well as the relevance and priority of their application. Finally, over-parameterization is a constant threat that needs to be guarded against and the related issue of excessive parameter sensitivity is often cited as a problem, however the problem also exists in the tools of demography, perhaps more so. (Breckling, Middlehoff & Reuter, 2006)

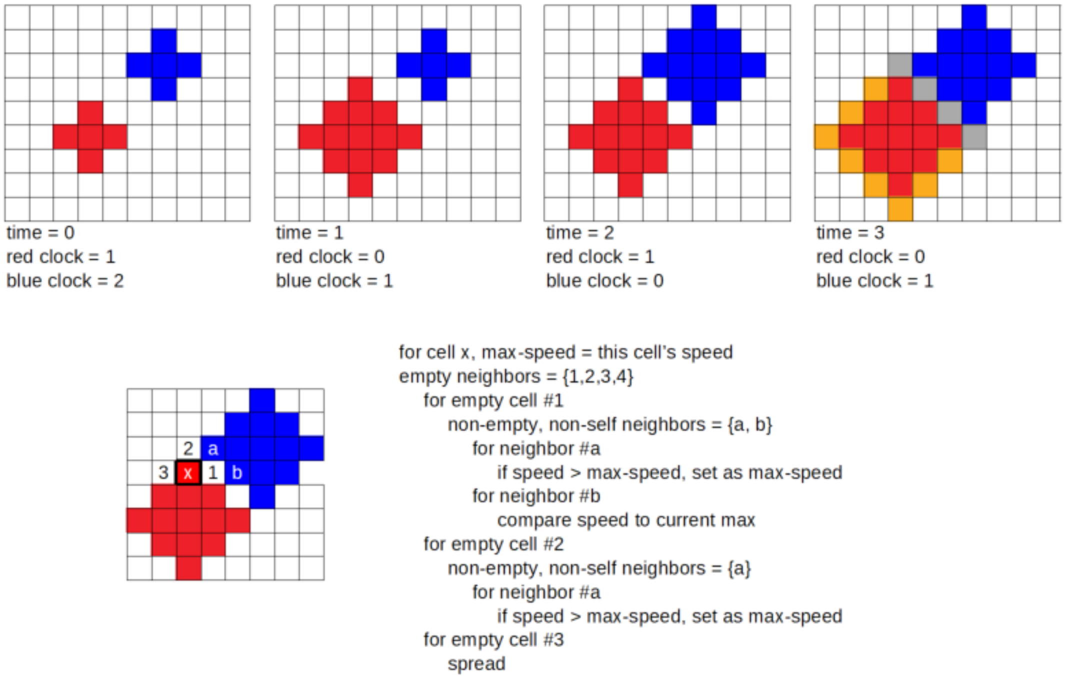
The main goal of spatial simulation is to achieve structural realism which is to make models reproduce observed patterns for the right reasons instead of forcing the right output via calibration. Pattern-oriented modeling is a general strategy to achieve this structural realism. Multiple patterns at different scales are used as filters in model design. The idea is to construct a model with a suitable level of complexity and so use the ability to generate the detected patterns as validation of the structural realism. Using the decoupling inherent in the encapsulation afforded by modern computing methods, we can write smaller sub-models that compute individual behaviors and activities in various ways, and then efficiently exchange them between successive model executions. Hence, we can structure our search for realistic mechanisms as a hypothesis-testing approach, posing alternative submodels for individual-level activities and falsifying them if they do not reproduce patterns observed at higher levels. This corresponds to the rationale of "strong inference" introduced by Platt (1964) for theory development (Grimm, 2017). Further, emergence requires that we represent heterogeneous environments and the use submodels of allows key behaviors of individuals that are based on first principles. (Grimm & Berger, 2016).

Spatial Model

In order to evaluate the effect of environmental variability on species coexistence, I propose to follow in the direction started by (Adler et al., 2006). The approach of using spatially-explicit individual-based models was abandoned by them in subsequent works, replacing them with integral projection models and other tools. This was perhaps due to that those individual-based models lead to an error in their conclusions that was retracted in the following publication. The error was due to structural assumptions implicit in their rules, although subtle it proved consequential. Their experience notwithstanding, I see much promise in the use of spatially-explicit individual-based models as a "virtual lab". The idea is to leverage data analysis tools on data from experiments or observations, extract a signal that we can amplify by spatial simulation and use in theory development cycle. To this end, I designed a model to reflect the spatial and temporal dynamics of colonial sessile organisms in a dynamic variable environment. The model is articulated to represent life history traits and lateral growth with neighborhood competitive and preemptive interaction. Reproduction reflect the dual traits of "brooders" whose juvenile disperse to a local neighborhood only and "spawners" whose juvenile disperse to the entire grid. Recruitment within those areas is purely lottery. Importantly, if the model is run with execution flags set to turn off lateral spreading, the model reduces to the same lottery model used by Chesson in the first study (Chesson & Warner, 1981) and by so many others. The patterns initially identified to validate the model structure were (1) spatial zonation along gradients of environmental parameters, (2) spatially autocorrelation of species with local dispersal, (3) lack of complete inter-digitiation of individual, leaving unoccupied gaps along boundaries and (4) differences in lifetime and mortality trends based on life history traits. Full details provided in the appendix.

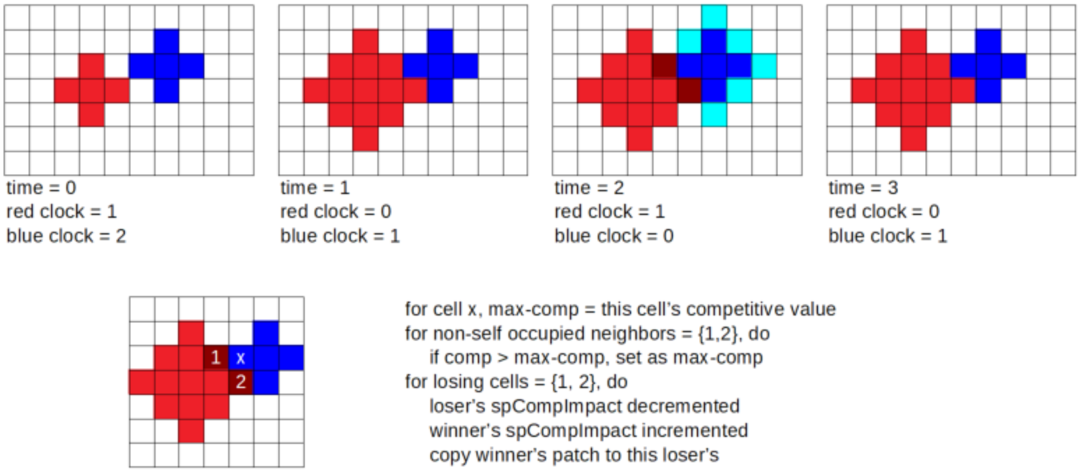
Importantly, the model was designed to provide an element of buffering to the populations. At the physiological level, there is a *Tolerance* attributes simulating the capacity to store resources, examples include fat and energy reserves in animals, carbohydrate storage in plants or food hordes accumulated by rodents. At the inter-annual level, a simple provision of a *Age Refuge* was implemented, corresponding to an features observed in nature of hibernation, torpor, diapause or other dormant stages, highly resistant to the harshness of the environment.

Spatial interaction, as a focal point of the model, were implemented to represent preemption of and competition for space by individuals. As depicted in Figure 4, during growth, a open site adjacent to multiple growing individuals is colonized by the individual with the highest *Growth Speed Rank*, as a form of preemption, alternatively, an occupied site adjacent of a growing individual is aggressively attacked as a form of competition and success goes to the individual *Competitive Rank*, as in Figure 5. During reproduction competition is by preemptive lottery, juveniles in the local pool disperse by lottery to any open site, while juveniles brooded by a parent disperse only to the local neighborhood.



```
for cell x, max-speed = this cell's speed
empty neighbors = {1,2,3,4}
    for empty cell #1
        non-empty, non-self neighbors = {a, b}
            for neighbor #a
                if speed > max-speed, set as max-speed
            for neighbor #b
                compare speed to current max
    for empty cell #2
        non-empty, non-self neighbors = {a}
            for neighbor #a
                if speed > max-speed, set as max-speed
    for empty cell #3
        spread
```

Figure 4: Algorithm for lateral spread.



```
for cell x, max-comp = this cell's competitive value
for non-self occupied neighbors = {1,2}, do
    if comp > max-comp, set as max-comp
for losing cells = {1, 2}, do
    loser's spCompImpact decremented
    winner's spCompImpact incremented
    copy winner's patch to this loser's
```

Figure 5: Algorithm for spatial competition.

An illustration of a model run showing all designated patterns is presented in Figure 6. It shows an elevation gradient with two bands of zonation (red and blue) as well as two areas of exclusions (at the very top and the very bottom). In addition, the continued presence of gaps between the colony, even within the same zonation bands, caused by the preference of a round shape of the spreading individuals, allows for on going recruitment in those gaps. And finally we noted the enlarged size of the red individuals relative to the blue, a direct consequence of the life history traits. This is the goal of pattern-oriented modeling, validation and reassurance by the matching of model output to multiple different patterns.

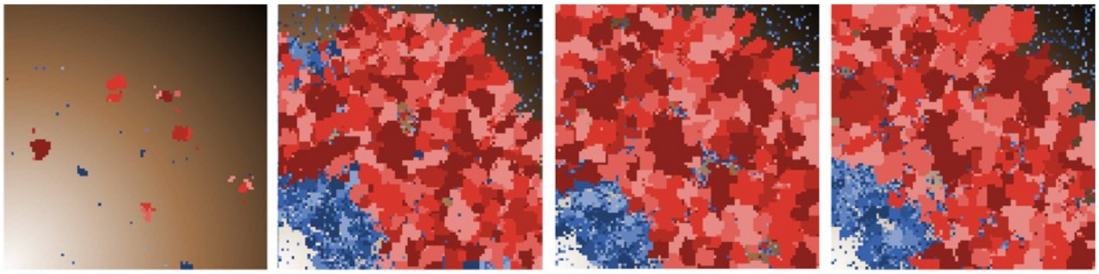


Figure 6: Illustration of a model run of two species showing all designated patterns.

The ability to control model execution so as to achieve scheduled immigration and mortality events allows the establishing of scenarios needed for running invisibility analyses. For example, a question regarding how ability of each species to recover from low density in the presence of the other was affected by changes in the environmental gradient could be answered by setting up an sequence of model runs as in Figure 7.

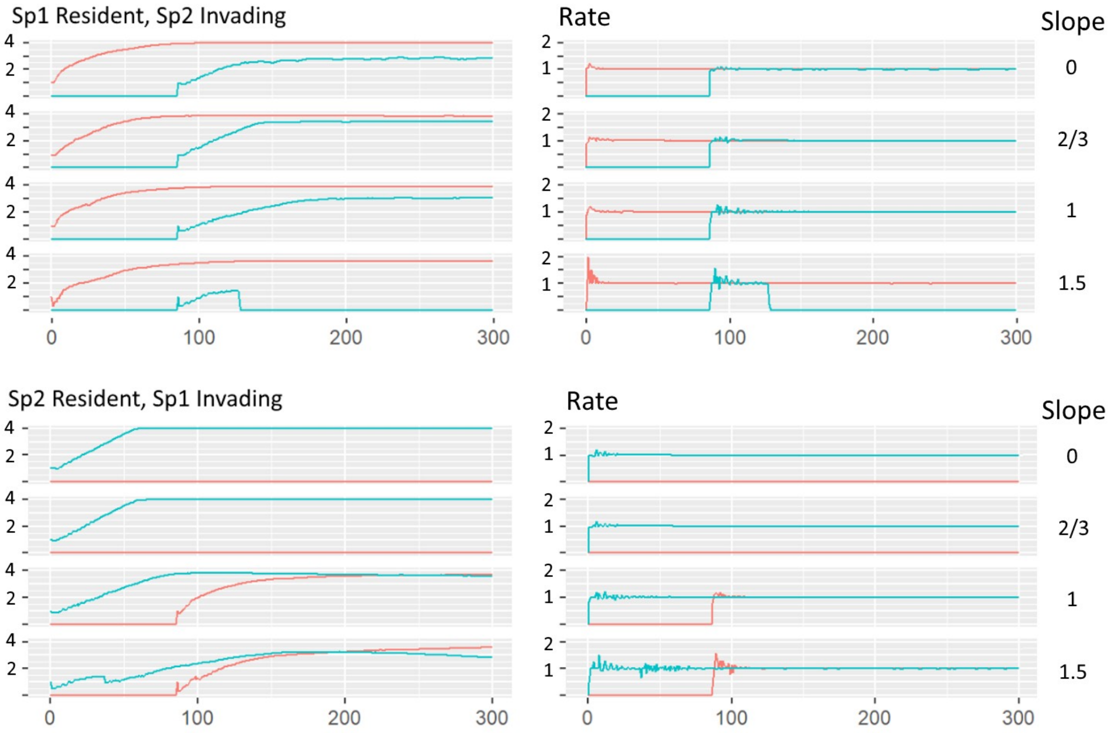


Figure 7: Log area and rate of log area for mutual invasibility on a varying gradient. Slope is determined as distance from the origin multiplied by a scalar coefficient (shown).

The traces in the plots in Figure 7 illustrate the ability of species 2 to recover in the presence of species 1 while the gradient is low to moderate, but we see a lessened ability to recover once the gradient reaches higher levels. On the other hand, species 1 is unable to recover in presence of species 2 without the presence of a significant gradient. Coupled with the ability to exchange the relevant submodels that control the individual behavior, the iterative nature of this modeling process is well-suited to the hypothesis-testing approach of pattern-oriented modeling.

Appendix: Code Narrative

Description

- Takes parameter sets defining community models, species, and time & space environment
- Takes jobs of model sequences specifying [label, run count, prm & time & space files, init pops, events]
- Instantiates individuals of each species within the specified community
- Runs agent-based simulation of community development over time
- Incorporates life history traits, demographic stochasticity, spatial interactions & env variability
- Maintains an event queue, capable of immigration, mortality and termination
- Outputs 2 levels of logging details to text files at each time step
  - each population's count and area
  - each individual's detail

Community

consists of
- the space, the time
- the environmental parameters
- the individuals, the juvenile pools
- the scheduled events

- growth rate limitation occurs by spatial interaction

Model Setup

loading a model involves loading the csv file and extracting
- model job file
- community prms,
- temporal & spatial env data

a model job is [label, run count, comm file, time file, space file, init pops, events]

this is done in the setup-model procedure
- the 3 files are are loaded by setup-model-prms
- the event queue is setup with setup-model-events
- the world is setup with setup-model-grid
- initial conditions are started by setup-community-from-pools

the model is now ready to run as per its event queue

also setup is the logging system
- community-level logs are a list gAbundanceList & gAreaList
- individual-level logs are in a list gIndividualsList
- all generated filenames are kept in gCommunityLogs & gIndividualsLogs

write about gRunCount gEntryCount gNextEventTime

Reproduction

2 modes: spawning and brooding

Spawning

when a colony is ready to spawn
- it makes decision whether or not to actually spawn
- it generates its offspring incurring a cost to do so
- it disperses the surviving offspring to the juv pool
- juvs mature and recruit from the pool

Brooding

when a colony is ready to brood
- it makes decision whether or not to actually spawn
- it generates its offspring incurring a cost to do so
- the broods disperse by jumping randomly to an open edge site
- the broods disperse further by jumping randomly to an open site in a cone
- if juvs survives, it recruits

Individuals

A timestep for an individual
- sense environment to set demographic values
- increment clocks
- mortality check
- spread
- reproduce & recruit

Individual's values
- Repro
  - spFecundity / 10
  - spReproTime [+/- 2]
  - spJuvMortality /100
- Growth
  - spCompetitive [normal(SD=1)]

  - spGrowSpeed [normal(SD=1)]
  - spMortality / 100
- Other
  - spTolerance
  - spAvRadius [+/- 1]
  - spColor [+/- 2]

Clocks
- spReproClock, spGrowClock, spAge: -1 at everytick

Env Response
- Individual's env response varying by a step function
- growth as function of size

Sensing
- sense environment
- find neighbors
- find non-self neighbors
- find non-species neighbors
- find empty neighbors
- find disconnected patches

Ecological Processes
- Relates <u>fitness</u> to env response and age
- Relates cumulative fitness to current and previous fitness
- Models decision whether to grow, to reproduce and to die
- Tracks competitive impact over life
- Implements random draws for the <u>mortality</u> functions
- Scales <u>reproductive</u> output by size & age, by fitness and by juv mortality
- Increment <u>clocks</u>
- Implement <u>death</u> & abandoning of substrate

Reproductive output is figured by
- scaling the current reproductive value by the number of colonized sites
- scaling that number of offspring by juvenile mortality

Reproduction
- does brooding – offspring are spatially located
- does spawning – offspring are added to juv pool and randomly located

Spatial Spread
- competes with neighbors when trying to grow
- spreads laterally when trying to grow

Individuals experience the environment and base their performance on it
- fitness is based on env responses & an age refuge

- cumulative fitness is based on current and previous fitness

Patches

- Patches are sites of individual colonization
- They are colonized by adjacent patches or landing recruit

- They are able to sense and select from patch-sets (presumably nearby, but not necessarily)
  - find unoccupied site
  - find max competitive neighbor
  - max growth neighbor

- They are able to sense presence or absence of neighbors
  - adjacent empty patches
  - nonself occupied neighboring patch
  - nonspecies occupied neighboring patch
  - self occupied neighboring patch (connected)

- Patches spread into empty space or compete for occupied space which are resolved by sensing the
  - max comp neighbor

Abandon patch is considered a patch method (maybe move to community)
- calls the community method, drop-site-from-list
- reset the values

find-unoccupied-patch is considered a patch method (maybe move to community)
- chooses one-of with no owner

Data Access Layer

Import

- parameter files are generated external and read in as csv files
- files for Prms (Model, Species, SpEnvResponses), Time (light, motion), Spatial (elevation)
- error checking is done for each set of parameter

Retrieval

- getter for model, community and species prms
- getters for spatial env data: elevation & depth
- getters for the temporal env data: surface light, surface motion
- getters for spatio-temporal env data: light at depth, motion at depth
- displays for color by light, motion, depth

Details

Creation

- Individuals are setup by setup-individ
  - takes the species prms
  - assigns values adding scaling & stochasticity

Env Response Functions

Light
- floor function, individual dies if value < threshold
- value is transformed, statistic = [threshold - value]
  - eg, individ can survive down to light levels of 2,
  - far above [threshold = 2, value = 5] so [statistic = 2 – 5 = -3]
  - close [threshold = 2, value = 3] so [statistic = 2 – 3 = -1]
  - below, die [threshold = 2, value = 1] so [statistic = 2 – 1 = 1]

Motion
- ceiling function, individual breaks if value > threshold
- value is transformed, statistic = [threshold - value]
  - eg, individ can survive up to motion levels of 4,
  - far below [threshold = 4, value = 1] so [statistic = 4 – 1 = 3]
  - close [threshold = 4, value = 3] so [statistic = 4 – 3 = 1]
  - above, die [threshold = 4, value = 5] so [statistic = 4 – 5 = -1]

- then statistic is acted on by env response function, implemented as step function
- floor vs ceiling is implemented as direction parameter where [floor = -1, ceiling = 1]
- direction is used to change the sign of the difference statistic
- the cut offs are hard-coded as 0, 2, 3
- the response at each levels is specified by parameter

Appendix: Pseudo-Code

Community DAL

Retrieve

get-pop-list

- iterate over species
  - call individs-by-species
  - call area-by-species

area-by-owner

- counts patches by owner-str

get-species-names

- iterate over species
  - return list of names

Sensing

find-individs-to-grow

- get all individs with non-positive spGrowClock
- filters by ready_to_grow?
- sort by growth speed

find-individs-to-repro

- get all individs with non-positive spReproClock
- filters by ready_to_reproduce?
- sort by fecundity

find-all-disconnected-patches

- reset all patches' flag
- ask each individ
  - append disconnected patches to a set to be returned

find-all-orphaned-patches

- ask each patch
  - if is-orphan, then add to a set to be returned

find-unestablished-individs

- find newly created individuals with no patches assigned

Processes

Overall

<u>do-community</u>
- for all turtles
  - sense-env
  - set-demographic-values
  - do-increment-clocks
- for all turtles, do-mortality
- spread-with-neighbors
- do-reproduction
- clear-stragglers

<u>do-events</u>
- do parse-event-str and assign names
- branch on event-label and call function with args
  - do-immigration-event
  - do-mortality-event
  - do-terminate

<u>do-terminate</u>
- nothing yet

Recruitment

<u>setup-community-from-pools</u>
- for each species in model,
  - call do-species-spawn
  - find-unestablished-individs for new individuals, for each
    - establish-individ-in-area in all-patches

<u>create-new-individs</u>
- create-turtle the passed in count
- run set-individ-values

<u>establish-individ-in-area</u>
- call find-unoccupied-patch on passed-in patchset
- if found, establish-individ
- if not, do-die as 'preemption'

Reproduction

<u>do-reproduction</u>
- filter on find-individs-to-repro
- branch on spReproMode
  - call do-colony-brooding
  - call do-colony-spawning

- reset repro clock
- setup-community-from-pools

reset-all-individs-growth
- for all turtles,
  - get figure-growth-clock
  - set grow clock

Community Spatial

spread-with-neighbors
- reset all patches
- call find-individs-to-grow
- if gDoSpread, do-all-spreading "spread"
- if gDoCompete, do-all-spreading "compete"
- do reset-all-individs-growth

do-all-spreading
- if "spread", then set flags
- for each turtle in passed-in set
  - check for the recently dead,
  - if spreading type, "spread" or "compete"
    - call do-colony-spread
    - call do-colony-compete

Reproduction & Interaction

clear-stragglers
- for each find-all-disconnected-patches, call abandon-patch
- for each find-all-orphaned-patches, call abandon-patch

Spatial Changes

add-site-to-list
- if not non-occupied, gain-colonized-site

drop-site-from-list
- if not non-occupied, lose-colonized-site

colonize-patch
- add-site-to-winner-list
- drop-site-from-loser-list
- change patch ownership and set-patch-values

Populations DAL

individids-by-species

- counts turtles by spID

area-by-species

- counts patches by substrate-str

Processes

Reproduction

do-species-spawn

- pull counts from juv pool
- create-new-individs if any
- reset juv pool for that species

do-immigration-event

- add-to-juv-pools

Mortality

do-mortality-event

- randomly select specified fraction of individuals to die
- call do-die with "event"

Individuals

Create

set-individ-values

- sets values from passed in prms, spXXX, spYY, etc
- adds stochasticity
- set turtle attribs and call setup-individual-clocks

establish-individ

- establish individual on patch with passed-in coords with setxy
- reflect individual's attributes to colonized patches, set-patch-values

setup-individual-clocks

- resets the clock and varying values

set-adult-attribs

- assign spAge, spReproClock, spGrowClock, spAvRadius

Retrieve

show-individ-sp-values

- compose string

show-individ-self-values

- compose string

count-colonized-patches

- check for non-existence, returns the number of sites in spSites

log-individ-values

Update

gain-colonized-site

- add site to spSites list

lose-colonized-site

- if not last site,
  - drop from spSites list
  - move turtle if needed
- if last site
  - call do-die

add-to-status

clear-status

Delete

do-die

- clear sites in spSites
- die

Sensing

find-sites-with-nonself-neighbors

- spSites with [any? find-nonself-neighbors self] find-sites-with-nonspecies-neighbors

- spSites with [any? find-nonspecies-neighbors self]

find-sites-with-empty-neighbors

- spSites with [any? find-empty-neighbors self]

find-disconnected-patches

- [find-connected-patches] of patch-here
- if has disconnected
  - (sense using flag to mark)

sense-env

- call get-env-values with xcor ycor ticks
- set spLightValue and spMotionValue

Env Responses

figure-age-refuge

- rectify negative values if above an age threshold
- if (pAge > 10)
  - if (pCumulativeFitness > 0)
    - if (value < 0), replace with 0.1

figure-env-response

- compare actual value to threshold
- flip sign depending on direction
- return value based on step function

figure-growth-clock

- figure effective radius
- set clock by comparing current size to sp-specific average

Individual Processes

these are grouped by that they sequence other functions to effect change in individual's state, they tend to be script-like

Fitness

do-responses

- do-light-response
- do-motion-response

do-light-response

do-motion-response

- get-env-reponse and use it to figure-env-response
- figure-age-refuge
- log reason if dead with add-to-status

Reproduction

generate-offspring

- if (incur-cost-of-repro)
  - set spReproOutput to figure-repro-output

do-colony-spawning

- if passes check-cost-of-repro,
  - generate-offspring
  - disperse-spawns

find-brooding-area

- if passed-in patchset is non-empty
  - move-to one-of passed-in edge sites
  - use find-empty-neighbors to find adjacent space, face one-of empty patch
  - detecting brooding area using in-cone
  - move back to original site

do-colony-brooding

- if (check-cost-of-repro?)
  - generate-offspring
  - if non-zero, do sprout-and-disperse-broods

Recruitment

setup-and-move-brood

- set-individ-values
- find-brooding-area
- if has brood area, in one-of patches, establish-individ-in-area
- else do-die status "preemption"

disperse-spawns

- add-to-juv-pools with spReproOutput
- reset spReproOutput

sprout-and-disperse-broods

- find open sites with find-empty-neighbors

- from parent's location, sprout # of spReproOutput, for each
  - setup-and-move-brood with open sites from above
- reset spReproOutput

Mortality

do-mortality
- if (spMortalityValue < 0), then
  - reason="other" & result = True
- if (spMortalityValue >= 0), then
  - resons = "demographic"
  - result = check-mortality?
- if so, do-die with set reason

Interact

do-colony-spread
- if incur-cost-of-growth
  - do find-sites-with-empty-neighbors , on those
    - if not already spread, do-patch-spread

do-colony-compete
- if incur-cost-of-growth
  - ifelse (gDoIntra)
    - do find-sites-with-nonself-neighbors
    - do find-sites-with-nonspecies-neighbors
  - from those, if not already, do-patch-compete

Individual Demography

idea here is to assign demographics values

Fitness & Clocks

set-demographic-values
- figure env responses, do-responses
- figure spFitnessValue, combine_env_responses
- figure_cumul_fitness
- scale_repro_value and scale_mortality_value

do-increment-clocks
- increment age

- decrement repro and grow clock

Reproduction

<u>incur-cost-of-repro</u>

```
• if (spCumulFitness > some-value)
    • spCumulFitness = (spCumulFitness - 2)
• return success flag
```

Growth

<u>incur-cost-of-growth</u>

```
• if (spCumulFitness > some-value)
    • spCumulFitness = (spCumulFitness – spGrowSpeed)
• return success flag
```

<u>do-competitive-impact</u>

- increment spCompImpact for winner, decrement for loser

Mortality

<u>filter-by-juv-mortality</u>

- get draw by juv-mortality-fraction
- scale repro output by draw value

<u>check-mortality?</u>

- result = (pMortValue < (random-float 1))

Adaptive Decisions

<u>ready_to_reproduce?</u>

- ((spReproClock <= 0) and (spReproValue != 0) and (check-cost-of-repro?))

<u>check-cost-of-repro?</u>

- (spCumulFitness > 2)

<u>ready_to_grow?</u>

- ((spGrowClock <= 0) and (spMortalityValue != 1) and (check-cost-of-growth?))

<u>check-cost-of-growth?</u>

- (spCumulFitness > spGrowSpeed)

did_survive?
- (pCumulativeFitness > 0)

Individual Maths

idea of these is to calculate all the various values used

Fitness

combine_env_responses
- sum of (0.5 * value1 + 0.5 * value2)
- if > 5, replace with 5

figure_cumul_fitness
- toler-value = (6 – pTolerance)
  - if (toler-value <= 0) [0.1]   ; avoid divide by 0
  - if (toler-value = 1) [1.75] ; avoid divergence
- pFitness + (pCumulativeFitness / toler-value)
- if > 10, replace with 10

Reproduction

figure-repro-output
- total output is passed-in repro value scaled by size
- output goes thru filter-by-juv-mortality

scale_repro_value
- if (pSurvived? and (pCumulFitness > 0))
  - [set return-val (pCumulFitness * pFecundityConstant)]

Mortality

juv-mortality-fraction
- random-normal (mean = passed-in value, var = 0.05)

scale_mortality_value
- if (pSurvived? and (pCumulFitness > 0))
  - [set return-val ((1 / pCumulFitness) * pMortalityConstant)]

Patches DAL

Create

init-patch
- set attribs bSubstrate, bOwner
- set flags bSpread, bClusterFlag

Update

set-patch-values
- set values pcolor, bSubstrate, bCompeted

color-by-elevation
color-by-depth
color-by-light
color-by-motion

abandon-patch
- do drop-site-from-list
- init-patch
- color-by-elevation

Retrieve

is-orphan?
- ((bOwner != 0) and (bClusterFlag = 0))

Sensing

Patchset Sensing

find-unoccupied-patch
- for passed-on patch-set
  - return one-of with [bOwner = 0]

find-max-comp-neighbor
- find neighbors occupied by non-self individuals
- iterates over them comparing competitive values
- reports winner and set of losers

find-max-growth-neighbor
- find neighbors that are empty and ready to spread
- iterate over them, compare
- report winner

--- Patch Sensing ---

find-nonself-neighbors

- for passed-in patch
  - get neighbors with nonself and non-empty attributes

find-nonspecies-neighbors

- for passed-in patch
  - get neighbors with different species and non-empty attributes

find-empty-neighbors

- for passed-in patch
  - get neighbors with empty attributes

find-connected-patches

- start recurse-connected-patches

recurse-connected-patches

- set bClusterFlag 1
- add to return set
- recurse to neighbors

Interact

do-patch-spread

- for each empty neighbor,
  - call find-max-growth-neighbor
  - call colonize-patch for winner

do-patch-compete

- call find-max-comp-neighbor
- if winner,
  - do do-competitive-impact
  - call colonize-patch

Model DAL

Create

initialize-model

- inits global values & constants
- call reset-community-log and reset-individ-log
- initialize-test-values

initialize-model-vars

- set values

initialize-model-pointers
- set values

initialize-test-values
- set values

Retrieve

show-model-values
- build string from model prm values

show-init-pools
- build string from get-init-pop-list

show-juv-pools
- build string from get-init-pop-list

get-init-pop-list
- gets vector of initial pop for each species

get-init-area-list
- gets vector of initial pop for each species

Update

set-env-prms
- set timeseries, gLightList and gMotionList
- set scalars, gRunDuration
- set spatial series, gDepthList
- set scalars, gMinDepth, gMaxDepth, gMaxExtent

set-model-prms
- resize world dimensions if needed
- set the gDoSpread, gDoCompete, gDoIntra

set-species-prms
- get & combine sp values and sp env responses
- set gSpCount to number of prms
- set gSpPrms to global list

set-all-prms
- use set-env-prms, set-model-prms, set-species-prms

Delete

clear-world
- clear-turtles, clear-all-plots, reset-ticks
- clear gRecruitsInput
- for all patches, call init-patch

reset-world
- call clear-world
- for all patches, call color-by-elevation

Processes

setup-single-model
- uses load_models_list to load the locs
- unpack the single item list and calls setup-model

setup-model
- clear-world, clear-output
- initialize-model
- call setup-model-structures
- call setup-model-grid
- setup-community-from-pools

setup-model-structures
- pass 3 files to setup-model-prms
- do init-juv-pools
- setup-model-events and set gNextEventTime

setup-model-prms
- get and save paths in gCommunityFile, gTimeFile, gSpaceFile
- load community, time and space prm files with load-csv-file
- do check-csv if passes, call set-all-prms

setup-model-events
- call enqueue-event add end event
- call enqueue-event add prm events

setup-model-grid
- resize world if needed
- for all patches, set bDepth by get-depth-by-coords & color-by-depth

instrument-job
- set gJobFile and call load-models-list
- reset gEntryCount
- for each (model in job),
  - do instrument-model

instrument-model
- increment gEntryCount & reset gRunCount
- for the (# run-count)
  - increment gRunCount
  - setup-and-run-model
  - output-all-logs and add-log-filenames

setup-and-run-model
- setup-model
- log-start and display-start
- iterate-model

iterate-model
- reset-ticks
- while (more-events?)
  - iterate-model-leg

iterate-model-leg
- while (ticks < gNextEvent)
  - do-model-step
  - log-timestep
- do-events with dequeue-events
- set gNextEvent & gNextEventTime

do-model-step
- tick
- do-community

Model Structures - Juv Pools

init-juv-pools
- for each spCount
  - set juvenile pool value to passed-in pInitPops

add-to-juv-pools
- increment values of the juvenile pools of specified species by passed-in amount

juv-pools-from-input
- look for non-empty string in gRecruitsInput text box
- if correct type and size,
  - call init-juv-pools

clear-juv-pools
- set all to zero

Model Structure - Logging

Write to logs

add-to-output-list
- add passed-in vector to global string

add-invid-to-output-list
- add passed-in vector to global string

make-init-output
- add timestep to population vector and an area vector
- return as list

log-start

log-timestep

Output

output-community-log
- call make-community-log-filename
- call write-community-to-file
- call reset-community-log

output-individ-log
- call make-individual-log-filename
- call write-individs-to-file
- call reset-individ-log

output-all-logs
- calls output-community-log
- if gLogAll, calls output-indiv-log
- return file names as list

Clear

reset-community-list
- reset gAbundList and gAreaList

reset-individ-list
- reset gIndividsList

reset-community-log-files

reset-individ-log-files

Display

display-start

Model Structure - Env Data Lookups

get-depth-by-coords
- lookup depth at some point in space

get-surface-light
- lookup surface light value at some point in time

get-surface-motion
- lookup surface motion value at some point in time

get-env-values
- gets env values at passed-in time & space coords
- scaled to depth at those coords

get-light-at-depth
- scale by hard-coded literals

get-motion-at-depth
- scale by hard-coded literals

get-env-reponse
- looks up the response function for specified species & env parameter
- returns the whole row

File I/O Import

load_models_list
- load file of locations by load-csv-file
- build list of model locs using extract-csv-block

load-csv-file
- reads text file with read-data-file
- scan to find each block start and end
- pull block titles if flagged

- convert into lists of values using extract-csv-block

extract-csv-block
- extract relevant lines
- parse from csv

find-blank-lines
- iterate over all lines
- find the blanks
- return list of line pointers to blanks

read-data-file
- read all file using file-read-line

Retrieve

get-csv-value-by-name
- lookup by name

get-csv-species-prms
- lookup by species ID

get-csv-sp-env-prms
- lookup by species ID

Logging

Filenames

make-community-log-filename
- string operations to transform standard date string into filename

make-individual-log-filename

Output to Files

write-community-to-file
- clears file if exists
- opens, writes, and closes

write-individs-to-file

Parse Events

<u>parse-event-str</u>
- string manipulations

<u>make-event-str-end</u>
- string manipulations

Check

check-csv
check-csv-locations
check-csv-community
check-csv-time
check-csv-spatial
check-csv-model
check-csv-species
check-csv-sp-env-resp
check-sp-env-prms-values
check-csv-time-prms
check-time-prms-values
check-csv-time-data
check-csv-spatial-prms
check-csv-spatial-data

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