Can constraint closure provide a generalized understanding of community dynamics in ecosystems?

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Abstract

Ecological theorists have generated several yet unresolved disputes that try to untangle the difficulty in understanding the nature of complex ecological communities. In this paper, we combine two recent theoretical approaches that used together suggest a promising way to consider how evolutionary and ecological processes may be used to frame a general theory of community ecology and its functional stability. First, we consider the theoretical proposal by Mark Vellend (2016) to focus on a small set of higher-level evolutionary and ecological processes that act on species within an ecological community. These processes provide a basis for ecological theory similar to the way in which theoretical population genetics has focused on a small set of mathematical descriptions to undergird its theory. Second, we explore ideas that might be applied to ecosystem functioning developed by Alvaro Moreno and Matteo Mossio's (2015) work on how biologically autonomous systems emerge from closure of relevant constraints. To explore the possibility that combining these two ideas may provide a more general theoretical understanding of ecological communities, we have developed a stochastic, agent-based model, with agents representing species, that explores the potential of using evolutionary and ecological processes as a constraint on the flow of species through an ecosystem. We explore how these ideas help illuminate aspects of stability found in many ecological communities. These agent-based modeling results provide in-principle arguments that suggest that constraint closure, using evolutionary and ecological processes, explain general features of ecological communities. In particular, we find that our model suggests a perspective useful in explaining repeated patterns of stability in ecological evenness, species turnover, species richness, and in measures of fitness.

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Introduction

Ecological theorists have generated several yet unresolved disputes that try to untangle the difficulty in understanding the nature of complex ecological communities, including the question of whether the idea of a community in such systems is coherent. For example, questions about ecological community structure and how it is maintained have been argued about for over a hundred years. These questions are still taking their current principal divisions from camps first staked out by Clements (1916) and Gleason (1926) in the early decades of the 20th century: Are communities assembled non-randomly, conditioned on certain possibilities of co-occurrence and structured by general ecological regularities? Or, alternatively, are they more arbitrarily constructed, brought together by a complex combination of abiotic factors, available species pools, competition, and other ecological processes that suggest a strong element of contingency (Eliot 2007, Götzenberger, et al. 2012)?

Currently, there does not seem to be a unified body of theory and practice that explains most features of community structure. The hunt for generality has also been fraught (See Elliott-Graves (2018) for a detailed overview). Theories in the discipline often seem a piecemeal confederation of ideas that carve nature mid-bone, as it were. Often focused on specific natural systems that provide only limited empirical and theoretical support from other, differently structured, ecological communities. It is clear that the theoretical constructions used by ecologists have been instrumental in the development of research programs and have allowed progress in understanding community ecology. For example, Hubble's neutral theory has been able to give a mechanistic account to assist in understanding statistical regularities in forest tree distributions (Abeysinghe and Punchi-Manage 2020, Alonso, et al. 2006, Hubbell 2001).

However, even basic concepts in the discipline are often viewed differently by different research groups that are often divided into opposing camps. There are even debates about the usefulness of the concept of community ecology. For example, the following questions are still being debated. Ontologically, could ecological communities be considered individuals because they are often maintained through time in the same coherent way that organisms are (Bryant 2012, Collier and Cumming 2011, Huneman 2014, Marquet, et al. 2014, Odenbaugh 2010, Odenbaugh 2011, Roughgarden 2009, Sterelny 2006, Sutherland, et al. 2013, Vellend 2016)? Which ecological theories best describe the dynamics of community structure, maintenance, resilience, and development (Chesson 2008, Kirchhoff 2010, Marquet, et al. 2014, Odenbaugh 2011, Roughgarden 2009, Sutherland, et al. 2013, Vellend 2016)? Do ecological communities have boundaries (Bryant 2012, Haber and Odenbaugh 2009, Peck 2009). Are they stable; what allows the coexistence of their constituent species (Chesson 2018, Hubbell 2001, Jeltsch 2019, Odenbaugh 2011)? How are communities linked as metapopulations and metacommunities (Chase 2005, Hanski and others 1999, Hanski, et al. 2017, Leibold, et al. 2004)? How are communities assembled? And are they so contingent that each community must be examined as an individual case study (Chase 2003, Rosindell, et al. 2011, Shrader-Frechette and McCoy 1994, Simberloff 2004, Vellend, et al. 2014, Weiher, et al. 2011, Wennekes, et al. 2012)? Are ecosystems real, constituent parts of nature, or are they merely constructed as an organizing principle to allow scientific study (Odenbaugh 2007, Sterelny 2001)?

These questions are all interrelated, yet the abundant theories used to tame and understand these ecological systems rarely provide a unified or coherent picture among theories. Moreover, in order to make progress in the idea of an ecological community, it seems essential to discover generalities that hold across the numerous possible biotic configurations that comprise these individual community assemblages. It is also important to view this project from multiple perspectives in order to tackle the inherent complexity and provide a more coherent picture among theories to create a more integrated conception of community ecology. There have been many attempts to do so, and the importance of these efforts recognized (de Mazancourt, et al. 2013, Evans, et al. 2013, Heleno, et al. 2014, Linquist 2015, Linquist, et al. 2016, Loreau and de Mazancourt 2013, Odenbaugh 2011, Roughgarden 2009, Simberloff 2004, Vellend 2016), though conditioned on some skepticism about the possibility of finding well-supported law-like regularities in community ecology (Lawton 1999, Lockwood 2008, Shrader-Frechette and McCoy 1994, Woodward 2001).

In this paper, we combine two recent approaches that used together suggest a promising way to consider how communities are structured, and which may offer the potential for a more generalized theory. In the first approach, we consider a proposal by Vellend (2016) to focus on a small set of high-level processes that provide a basis for ecosystem theory, similar to the way that theoretical population genetics has been fashioned to focus on a small set of processes with relatively simple mathematical formulations. Vellend proposed that we look at ecological communities in light of four evolutionary and ecological processes found in a wide variety of ecosystems: species selection, species-drift, dispersal, and speciation (Vellend 2010, Vellend 2016). These community-level processes focusing on species are thought to capture the means whereby most ecosystems are structured.

In the second approach to consider how communities are structured, Moreno and Mossio (2015) show how constraints on the flow of matter and energy enable the development of autonomous, self-sustaining, stable structures in chemical and cellular systems. We use their concept to explore the idea that constraints may similarly configure large-scale processes, like the flow of species through an ecological community, to create semi-autonomous, self-sustaining, stable structures in ecosystems (for other attempts to argue this approach, see, (Dussault and Bouchard 2016, Huneman 2014, Montévil and Mossio 2015, Moreno and Mossio 2015, Nunes-Neto, et al. 2014).

By combining these two approaches and perspectives, we argue with support from agent-based simulation models, that this might be a productive way to explore general features of stability in ecological communities. We also use the idea that a useful way to think about ecological communities is using trait-based assemblages that focus on trait functional diversity rather than individual species as components of communities (Fontana, et al. 2016, Petchey and Gaston 2002, Zakharova 2019). For example, beak size in Galápagos finches reach a certain size and shape among the different islands, presumably because they use food resources that require particular beak traits. Rather than thinking about species as taxonomic units, species are represented as functional groups based on specific traits. Trait-based functional groups were used by Carturan et al. (2020) to model community dynamics of coral reefs using an agent-based model. We will use a similar approach in our model.

Trait-based approaches to species groups has especially useful in creating morpho-species in biological samples taken from a large number of organisms in which species' identifications are difficult, such as in satellite images of forest (Schneider, et al. 2017), in logistically hard to sort through samples like dragnet catches of phytoplankton (Salmaso and

Padisák 2007, Weithoff and Beisner 2019), other plants (Armbruster, et al. 2002) and animals (Derraik, et al. 2002), and in computer simulations (Marks and Lechowicz 2006). Morpho-species based on functional groups will be used in work described below.

Constraint Closure

One way to approach the general idea of an ecological community can be drawn from Moreno and Mossio's (2015) work on biologically autonomous or semi-autonomous systems. This paper proposes their work, largely based on cellular and chemically reproducing systems, may be relevant for ecological communities. They identify three dimensions of general biological autonomy: regulation, stability, and historical contingency. Because ecosystems are more permeable in terms of their structure and boundaries, it may be more appropriate to consider them as semi-autonomous, which allows for less well-defined and fuzzy boundaries.

The first dimension of biological autonomy, or semi-autonomy (i.e., regulation), of an ecological community, is structured by three things: (a) its abiotic context; (b) the ecological processes that are characteristic of a particular ecosystem, including the boundaries that contain or restrict the flow of energy within the ecological system (e.g., conditions of a lake ecosystem are bound by its shore and inputs through streams), and (c) the processes that allow for the particular conditions to be maintained through internal cycles of biotic components within the system through time (e.g., predator-prey cycles, or the self-maintaining light regime of a tree species growing in a forest).

According to Moreno and Mossio's (2015) work, constraint closure is necessary for autonomy or semi-autonomy to emerge. Constraint closure is described as constraints on the flow of matter or energy that form a closed loop and thereby allow for the development of stability. This is a necessary step in the formation of all autonomous systems. Such a configuration of constraints creates a sustainable feedback loop that allows the system to achieve coherence. Constraints emerge from the system processes themselves (e.g., through developmental processes, autocatalysis, or in cellular processes). Fig. 1 illustrates a minimal set of requirements for the occurrence of constraint closure and illustrates how such components modulate the flow of energy and materials within the system; redrawn from Figure 1.3, p. 21, (Moreno and Mossio 2015). Moreno and Mossio (2015, 38) point out that regulation is just a step on the way to autonomy so the ideas of autonomy and regulation have an important distinction.

The second dimension of biological autonomy, or semi-autonomy (i.e., stability), is found in interactions conditioned on the larger environment that provides the energy and materials used by the system. In an ecological community, these interactions can take the form of energy flows from sunlight or the movement of organisms in and out of the ecosystem. Such flows might also include forces of disturbance that might restructure the system through things like direct human influence, invasive species, diseases, or abiotic influences such as fire, weather-related events, and other non-biological influences.

The third dimension of biological autonomy, or semi-autonomy (i.e., historical contingency), includes the system-specific historical and often contingent aspects of the system. For example, in an ecosystem, it might include the past arrival of new species, ecological processes that have emerged due to the interactions of local configurations of constitutive species, evolutionary dynamics, contingent factors, co-evolutionary adaptations, and other biotic and abiotic influences (Spencer 2020).

Given the above, and, as Moreno and Mossio (2015, 105-108) speculate, there are reasons to think that ecological communities might be autonomous or semi-autonomous systems. The energy flow is maintained and channeled within the system by its components. For example, long-term community stability has been shown to be structured by a number of well-studied ecosystem processes, such as the competitive exclusion of species restructuring particular niches, networks of mutualistic relations, and typical ecological interactions like predator-prey relations.

Nunes-Neto et al. (2014) make an argument that ecological communities can be seen as autonomous systems because of the functional components of traits that structure most ecosystems. In particular, they look at the function of the components of biodiversity using what is termed the 'organizational approach' (OA) that they use to argue for biological autonomy and stability through constraint closure. Dussault and Bouchard (2016) add a significant consideration to the above account, developing a focus on particular kinds of functions that they call persistence enhancing propensities (PEP). PEPs are a class of functions that allow the currently structured ecosystem to persist stably. The technical details of OA and PEP functions are given in Appendix 3.

Vellend's Set of Processes as Constraints

By combining the above ideas articulated by Moreno and Mossio about autonomy with Vellend's proposal to focus on four high-level processes structuring species dynamics within a community, we can see a possible theoretical space open by combining the two views to consider the ways certain constraints may stabilize ecological communities. It might reasonably be argued that the processes Vellend identifies, species selection, species-drift, dispersal, and speciation, constrain and structure the 'flow of species' through an ecosystem. Each of the four processes that Vellend identified restrict, modify, or enhance the flow of species, and thus act as constraints on the system. Because the constraints that Moreno and Mossio discuss are not limited to the kinds of structures typically discussed in the flow of matter and energy in chemical or cellular systems, it is not unreasonable to consider the potential of constraint closure to organize ecological communities in the way they discuss for chemical systems. It might be objected that this type of analogy in which evolutionary and ecological processes affect species flow through a community might not hold in the same way that systems of cellular or chemical processes maintain stability through constraint closure do. These basic physical systems have more well-understood mechanisms that constrain the flow of energy in material systems that might not hold in ecological systems. Therefore, stretching the notion of constraint closure to something as complex and multivalent as evolutionary and ecological processes that act on individual species and their flow should rightfully be approached with caution. However, we believe that the results describe below provide warrant.

Consider that in Vellend's four processes, selection constrains the success of a species by affecting its ability to compete in its current abiotic and biotic situation and providing fitness conditions for the species' success or failure in surviving in a particular environment. Species-drift constrains the population genetic structure and what variation is available to a community's individual species, and how stable the presence of a species is in a bounded region, including how it drifts in adjusting or modifying its current niche conditions. Speciation, in addition to the effects of selection, constrains how many new species emerge in an area due to genetic factors, and the interplay between trait differences and the biological fitness of those differences. Likewise, dispersal constrains species flow by influencing a combination of a species' ability to spread beyond its original location, for instance, in the sense that geneticist Sewall Wright proposed in his three-step shifting balance theory, that is, (1) initial establishment, (2) population growth, and (3) species dispersal of individuals to new areas (Pigliucci 2008). This suggests a hypothesis that these processes constrain ecosystem function.

Constrains on species flow through the system may set up such communities as autonomous or semi-autonomous systems through constraint closure analogous to the way Moreno and Mossio (2015) envisioned about how autonomous systems are maintained for a period of time. In particular, species and the ecological functional groups they define flow through a community frame as a set of persistence enhancing propensities that influence stability and other aspects of community dynamics. There may be other possible constraints on species flow. For example, things like boundaries over which species cannot cross may affect which species enter a particular community. The spatial patch dynamics of particular landscapes, such as the metapopulation structure, creates a constraint on species flow. Other processes like the frequency of disturbance and mutualistic relationships among species within an ecosystem, which affect the survival probabilities of cooperating species, may also play a role. In particular, mutualist relationships are a major influence on ecosystem dynamics and stability, for example, the mutualistic relationships in mycorrhizal networks (Booth 2004, Heijden, et al. 2015, Mnasri, et al. 2017, Peay 2016, Simard, et al. 2012, Yang, et al. 2014).

A Model of Constraint Closure in Autonomous Ecological Communities

To explore the possibility of using constraint closure to understand ecological communities, we developed an agent-based model that explores the potential of understanding the semi-autonomy and stability of ecological communities as an effect of constraints on the flow of species through the ecosystem. We provide in principle arguments that constraint closure may be a way to structure general insights into measures stability in some ecological communities.

Brief Model Summary

A complete, detailed model description that follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm, et al. 2006), as updated by (Grimm, et al. 2020), is provided in the supplementary material in Appendix 1. The reader is encouraged to consult this section to understand the model more fully.

Briefly, the overall *purpose* of this model is to understand and provide in principle arguments about how evolutionary and ecological dynamics may be viewed as constraints that confer autonomy and stability through constraint closure in ecological communities. Specifically, we address the *questions*: Can combining the insights of Vellend's (2016) work on species evolutionary and ecological processes in community ecology and Moreno and Mossio's (2015) work on constraint closure be used to shed light on common characteristics of ecological community stability and autonomy? The model is designed to provide theoretical insights into ecosystem stability and provide motivation for ecologists to consider examining their particular systems for the kinds of constraints proposed here.

To consider our model adequate to its purpose, we hypothesize specifically that *patterns* of standard measures of community dynamics, such as species richness, evenness, and aspects of species fitness, will stabilize in response to evolutionary and ecological dynamics acting as closed loops of constraints. The fidelity criteria we aim for will be achieved if the model shows that such patterns of stability *emerge* in ways that suggest the included dynamics act as constraints in the way that Moreno and Mossio (2015) propose, that is, that these evolutionary processes are sufficient to confer known *emergent* attributes of autonomy or semi-autonomy, and stability on the ecological community. We make no claim that this model will represent any specific target system but that it will provide insight into general ecological systems. If the results of this model hold up in real-world ecological systems, it will generate testable hypotheses about how particular ecosystems function.

The model includes two kinds of entities, trait-based agents representing functional groups of morpho-species (referred to as 'species' in the following) and cells representing niches in "niche space", not physical space (Fig. 2). Each cell represents, quantified by a single number (dubbed niche score) the set of possible trait-based functional groups or 'species slots' that could occupy this niche. This niche is thus not a classical one-dimensional niche but represents a more complex set of environmental configurations that are suitable for certain a suite of species. Each species found in a cell represents a single trait-based functional group that finds the niche (cell) habitable. The number of species that a cell can hold is limited, implying that the cell niche can only hold a given number of species.

Movement of species in niche space is restricted to the eight neighbor cells. Species differ in niche preference, and each species has a preferred niche, also characterized by a single measure called the niche-desirability score. The extinction probability of a species is defined as the absolute difference between the cell's niche-score and the species niche-desirability score. The state variables of the cells and species are found in Table 1 and Table 2, respectively.

Evolutionary and ecological constraints: Table 3 gives a list and description of the proposed evolutionary and ecological processes thought to constrain the flow of species in an ecosystem and thereby produce ecological measures of stability. Constraints include the processes proposed by Vellend as well as adding two others: mutualism and ecological perturbation. The most important *constraints* of the model, which are repeated at each time step, and executed in the following order: establishing mutualistic networks of species, spatial dispersal to adjacent cells, competition among species and concomitant species extinction in the cell, species-drift, and lastly, the possibility of ecological collapse and perturbation (i.e., species loss irrespective of extinction probability).

Because the theory of constraint closure developed by Moreno and Mossio (2015) about autonomy and stability suggests that at least three constraints are necessary to create closure in the relevant sense, we examine in our analyses the number of constraints. We also examine the influence of each of the processes to assess how each of the constraints we included affects the outcome patterns of the indices of stability emerging in the simulated community. We have no a priori reason for thinking that one of the given constraints might contribute to ecological measures of stability more than another, so we first examine measures of stability against the number of constraints in our analysis.

We also analyze how each of the constraints contributes to the ecological stability measures using statistical random forest analyses to determine the evolutionary and ecological importance of each of the constraints (note: random forests are a statistical technique and do *not* refer to an ecotype consisting of trees). For each of the constraints, random forests were used on the individual outcomes as dependent variables. The constraints as independent variables provide information about a variable's importance. A good description of the use and evaluation of random forest analyses can be found in (Strobl, et al. 2007), but briefly, a constraint's importance was determined by calculating the mean standard error (MSE) for each statistical model of the data generated by the agent-based model outcomes. This is accomplished by randomly permuting one of the constraint outcomes and then calculating the percentage change from the unpermuted model (for example, comparing the model's MSE before and after shuffling the values for the variable *competition*). High values of importance indicate that a given constraint is necessary for maintaining model adequacy, while low values indicate that a constraint does not influence model error.

The basic *design concepts* in the model include evolution driving the *adaptation* of species to be more closely aligned with the niches represented within the cell they reside; the collective networks of species forming mutualistic relationships; and the emergence of stability through the process of evolutionary and ecological dynamics thought of as constraints imposing stability through constraint closure. The time step of the model is the average time to species extinction. See Fig. 3 for an illustration of the process flow in the model. Table 4 contains the parameters for the model.

Also important are the *stochastic* elements framed in the following ways: (a) the initial cell structure of the landscape is randomly generated; (b) The proportion of species chosen to form links is a random variable; (c) the species that become extinct in the drift stage are randomly chosen with probability proportional to a species' probability of extinction; drift is defined in terms of the species particular functional group in the cell (d) species with a low probability of extinction are chosen to move randomly to one of their 8-Moore-neighborhood neighbors; (e) The variation in the probability of extinction in newly speciated species is a random variable, and (f) the stochastic perturbation events of species going extinct due to dynamics other than their inherent probability of extinction.

Observations are collected from a Latin hyperspace exploration of the parameters described in Table 4 by taking random samples from the range of their possible parameter values in 2000 replications. The model was run for all 64 possible combinations of constraints, with each constraint being turned on or off for a complete characterization of the state space of the model with regard to the offered evolutionary and ecological constraints considered. The number of constraints included varies as these different permutations on the state space of the model are examined. Because we are looking for constraint closure, which requires at least three constraints, the number of constraints used is relevant for demonstrating the theory outlined above. Each run consisted of 500-time steps for each landscape produced in the combinations listed above.

The measures of stability examined in the model are species evenness, turnover rate, species richness, and fitness landscape as defined by the probability of extinction. Evenness was measured using a modified Pielou's evenness index, modified for algorithmic efficiency. Rather than the mathematical equation, $J' = \frac{H'}{H'_{max}}$ where H' is Shannon's Index, $H' = -\sum_{i=1}^{S} \frac{p_i}{\ln p_i}$, where p_i is the proportion of the i^{th} species, and S is the maximum number of species, we modify it as follows: Because the number of species per cell is fixed, the algorithm used is computed by the number of unique functional groups in a cell, divided by the number of species in the cell. This has the range $\left[\frac{1}{S}, 1\right]$, where the lower range is found in the case where every species in the cell is functionally unique, and the higher when there is only one species type. Turnover is modeled such that new species arise when there is an opening in relation to the packed niches of each cell. This opening occurs in two places: (1) when there is selection between the linked and unlinked species in which the least fit species is eliminated; and (2) in perturbation events when a large number of species go extinct without regard to their fitness status as might happen in a large natural disaster such as a wildfire.

Results and Discussion

These simulation results provide evidence that constraint closure may lead to measures of ecological stability through long-term evolutionary and ecosystem processes. It is evident that such processes included in the simulation model do affect the flow of species through the ecosystem in much the same way that Moreno and Mossio (2015) propose that stable autonomous systems are created by constraint closure. This model provides simulation evidence (see Parker (2021) for how simulations can be used as evidence (Parker 2020)) that certain evolutionary and ecological processes can, in principle, act as stabilization conditions and provide semi-autonomy in ecological communities.

In Fig. 4a, the effect of the number of constraints on fitness (defined as the extinction probability) can be assessed. We would expect as the average fitness among species across the community landscape of the model begins to evolve over time, that the average extinction probability decreases as the constituent species adapt to the conditions of the local cell in which they are found. As the number of evolutionary and ecological constraints increases, fitness increases, and the variation in fitness decreases. Two noteworthy results on fitness emerge: (1) without any processes present in the model run (The number of constraints = 0), the fitness stays at a baseline value; when all 6 constraints are present in the model, maximum fitness is achieved in the model. This suggests that the species flowing through the ecosystem are channeled by the candidate constraints creating constraint closure in the relevant sense that Moreno and Mossio outlined (Moreno and Mossio 2015).

The effect of the number of constraints on ecological evenness, as measured by the modified Pielou's evenness index described above, is given in Fig. 4b. As the number of constraints increases, the maximum mean evenness is achieved when there are three constraints present, which pattern mirrors the required three constraints that Moreno and Mossio (2015) argue are necessary to create constraint closure. Increasing the number of constraints causes the evenness to decrease, although not as low as when there are no evolutionary and ecological constraints present in the simulation model.

Fig. 4c evidences that the effect of the number of constraints on the species richness (based on the number of functional traits present in the cell) averaged over all the cells making up the community in the niche-cell. Species richness reaches a minimum when there are three constraints and then increases with added constraints. The species richness has lower numbers of species creating depauperate within-cell diversity as the number of constraints increases. This shows species richness increases with added evolutionary and ecological constraints as these constraints affect species flow. So while individual cells may trend toward being more uniform within the cell, landscape richness maintains variation. For example, from Fig. 4c, it is clear that as the number of species shrinks and becomes < 10 species per cell, the overall community ecology of the entire landscape retains its variation in these functional groups.

The effect of the number of constraints on the difference between turnover in species with and without mutualistic relationships (linked and unlinked species) is provided in Fig. 4d.

The turnover rate is the number of new species created at each time step in each cell. The pattern is consonant with networked species alone, creating an increase in turnover rate due to selection.

Fig. 5a shows the percent increase in mean standard error (MSE) in a random forest model for landscape fitness when each constraint is removed. When all six constraints are present in the model, the maximum fitness is achieved. As expected, the MSE as constraint *selection* and *competition* are the most important processes for the overall fitness of the landscape.

The constraint with the greatest influence on *evenness* (Fig. 5b), was *species-drift*. As expected, as species drift away from parental type, *species-drift* strongly influences evenness measures, and structures the community through its influence on the set of constituent species. The evolutionary processes of *selection* and *competition* are also highly influential in structuring evenness scores, while *dispersal* and *mutualistic networks* are weaker influencers on *evenness* compared with *selection* and *competition*.

Similar to *evenness*, *species-drift* was the constraint with the greatest influence on *richness*, Fig. 5c. This makes sense as species drift from parental type, which in turn strongly influences the number of species. The evolutionary influences of *selection* and *competition* were highly influential in structuring richness scores, while *dispersal* and networks of *mutualism* were the least influential for similar reasons to evenness discussed above.

The pattern of constraint influence seen in the difference in turnover between species forming mutualistic networks and those not, Fig 5d. This pattern is consonant with networked species alone creating an increase in turnover rate due to *selection*, the second most influential constraint of interest. As *competition* is set up between species without regard to *mutualistic* relationships, it unsurprisingly drops to the lowest constraint of interest in the analysis.

Fig. 6, shows the effect of the number of constraints on the variance of landscape fitness. The pattern of mean distribution and the variance associated with the progression as the number of constraints increases is evident in the scatter of the variances.

One criticism that might be leveled in the above results is that species richness might achieve within-cell population sizes that are too low to be meaningful. While richness is often low in the simulated landscape with increasing constraints, the mean and median are such that a large proportion of low species diversity in the cell does not change the landscape variance in richness, as illustrated in Fig. 7. This also suggests that while individual cells in the ecosystem may become depauperate, the overall variation in diversity of species in the ecosystem remains remarkably consistent. This might have ecological reality, illustrating that if a set of niches within a community becomes dominated by a particular kind of species (e.g., a patch of forest becoming meadow), the ecological community does not necessarily become simplified to the point where low richness among the functional groups translates into low community richness. As can be seen, there is an almost consistent variance in the simulated community as the number of emergent constraints increases.

Further information on how each of the emergent constraints affects fitness singly and in interaction is found in Appendix 2, and in Fig. S1, S2, and S3.

Conclusions

The proposal that evolutionary and ecological processes can act as constraints in the appropriate sense that it creates autonomy (or semi-autonomy) and stability needs more theoretical and practical examination and development. This model is not a knockdown argument for evolutionary constraints acting on the flow of species and thereby structuring ecological stability. Even so, it is a starting point worth further thought and consideration. The work presented here points to the possibility that evolutionary and ecological forces might be explored as a possible source of stability in community ecology.

We believe the idea of combining Vellend-like processes with Moreno and Mossio's (2015) approach to autonomous systems has enough warrant to be productively explored by ecologists and other theorists and modelers. They might help formalize the structural arguments argued here to explore whether the analogy holds more rigorously. If these proposed evolutionary and ecological dynamics constrain species in the way we suggest, and to which our model points, then the structures of community ecology, such as stability and long-term persistence, should emerge as constant patterns due to specific evolutionary and ecological processes, suggesting a new research program for community ecology. In addition, such work may discover other general features of these systems that suggests constraint closure allows for their continuance.

The emergence of particular pattern formations also may imply empirical work that lends evidentiary support as to whether these evolutionary dynamics form propensity enhancing propensities in the right way to meet the criteria as defined by Dussault and Bouchard (2016) {Dussault, 2016 #29. Further work is, of course, needed to establish these informed speculations, but we argue here that it is warranted and may be highly productive.

Figure Legends

Fig. 1. Constraint Closure. Constraint closure is described as constraints on the flow of matter or energy that form a closed loop allowing the evolution of stability and autonomy. According to Moreno and Mossio (2015) this is a necessary step in the formation of an autonomous system. Such a configuration of constraints provides a sustainable feedback loop that allows the system to achieve coherence for a period of time, τ. In the original theoretical formulation by Moreno and Mossio these are envisioned to have causal effects on any processes that makes transformations from one condition to another. In the system depicted above, the A_i are processes, and the C_j's are constraints. The arrows indicate the flow of energy or material effecting causal changes to either the A or C system components indicated. Each vertical row of processes and constraints represent different times. The processes enclosed in the ellipse together form a closed-loop creating "constraint closure," producing stability, which serves as a foundation for the emergence of autonomy in the system. It is proposed that closed constraints may help stabilize ecological communities in which ecological and evolutionary forces act as constraints on species flowing through ecosystems on relevant time scales. Redrawn from Figure 1.3, p. 21, Moreno and Mossio (2015).

Fig. 2. Distribution of habitat (black) vs nonhabitat (grey) in model landscapes with the given parameter values of *spatial_habitat_patch_distribution_parameter_1* (SHP). See ODD section of Appendix 1 for details. Such random landscapes are generated in the initialization phase of the model. Fig. 2A, SHP = 2 ; Fig. 2B, SHP = 6; Fig. 2C, SHP = 12; Fig. 2D, SHP = 20.

Fig. 3. Flow of model. See ODD section of Appendix 1 for details. Process Flow within model. The agent-based model used in this paper cycles through Vellend's proposed higher-level ecological and evolutionary processes that operate in ecological communities, with the added ecological processes of mutualism, and periodic, catastrophic species loss. These structures will emerge as constraints to create semi-autonomous structures. The flow chart shows the order of events and possible flow paths taken in the model.

Fig. 4. The theory of constraint closure developed by Moreno and Mossio (2015) suggests that at least three constraints are necessary to create closure. In this figure, we focus only on the number of constraints and how they affect the given measures of ecological stability. Boxplots show ecological measures across parameter space for different numbers of constraints generated by 2000 iterations of the simulation model across all 64 possible permutations of the proposed constraints being present or absent, and with uniform random values of parameters pulled from their possible values in the model iterations. The whiskers in the box plot show the range of variation. The actual data used to construct the boxplots are shown fine gray dots to the right of each box plot. (a) Effect of the number of constraints on landscape fitness. (b) Effect of the number of constraints on ecological evenness. (c) Effect of the number of constraints on the average cell species richness (number of species defined as functional groups) present in the cell-niche. (d) Effect of the number of constraints on the difference between turnover in mutualistic linked and unlinked species. The turnover rate is the number of new species created at each time step in each cell.

Fig 5. Percent increase in mean standard error in a random forest model of ecological measures when each constraint is removed (see main text for an explanation of this statistical technique). This analysis gives a measure of the influence of each constraint on the model. (a) For *landscape fitness*, the mean square error (MSE) suggests *selection* and *competition* are the most important constraints for the overall fitness of the landscape. This is not surprising given that these constraints are well known to be directly tied to the ideas of fitness. (b) For *evenness* the percent increase in MSE in a random forest model, *Species-drift* was the constraint with the most influence on evenness. (c) For *species richness* the percent increase in MSE in a random forest, similar to *evenness*, *species-drift* was the constraint with the most influence on richness. (d) Difference in turnover rate measures the difference in *turnover* rate between species that can form mutualistic networks and those that cannot. The percent increase in MSE in a random forest model when each constraint is removed is consonant with *networked* species being the constraint with the most influence. *Selection*, is the second most influential constraint of interest.

Fig. 6. Effect of the number of constraints on the variance of average species fitness, defined as extinction probability, across the landscape and across parameter space. Boxplots show landscape variance for different numbers of constraints generated by 2000 iterations of the simulation model across all 64 possible permutations of the proposed constraints being present or absent, and with uniform random values of parameters pulled from their possible values in the model iterations. The whiskers in the box plot show the range of variation. The actual data used to construct the boxplots are shown fine gray dots to the right of each box plot.

Fig. 7. Overall landscape variation in species richness. Recall that richness in this analysis of model results is measured on the functional group of the species rather than the number of species. Because the cells represent packed niches, the number of species it holds is a constant. Boxplots show the landscape-level variance in the difference between the turnover in mutualistic linked and unlinked species. These differences are plotted against different numbers of constraints, generated by 2000 iterations of the simulation model, across all 64 possible permutations of the proposed constraints being present or absent, and with uniform random values of parameters pulled from their possible values in the model iterations. The whiskers in the box plot show the range of variation. The actual data used to construct the boxplots are shown fine gray dots to the right of each box plot.

Variable name	**Variable type and units**	**Meaning**
species_preferred_niche	Real number; range (0, 1)	A single value integrating a species niche requirement. This will be compared with cell_niche_score to assess the probability of a species extinction.
maximum_number_of_links	Integer, range [2, 100]	For species that can form links, the maximum number of links that it can form with other species.
current_number_of_links	Integer, range [0, maximum_number_of_links]	The current number of other species with which a species forms a link.
probability_of_species_extinction	Real number; range (0, 1)	The probability of extinction for a species based on the absolute difference between a species *species_preferred_niche* and the *cell_niche_score* on the cell in which it currently resides.
species_niche_function	Integer, range [1, maximum_number_speices_per_patch]	This identifies the trait-based functional group within a niche to which the species belongs.

Table 1: Species state variables

Variable name	**Variable type and units**	**Meaning**
cell location; the code uses NetLogo's built in coordinate variables	Real, static; scale is arbitrary and represents a scale of community size for an average number of possible species	The X and Y coordinates of the cells with origin in bottom left corner.
cell_niche_score	Real, static, range [0, 1), a value of 0 designates an uninhabitable patch	The cell-niche characterization by which species will be compared in assessing their extinction probability on a patch.

Table 2: Cell state variables

Model Constraint	**Description**	**Definition**
create_species_networks	Establishment and maintenance of mutualistic network of linked species within a cell. If this constraint is turned off mutualistic networks are not established.	This constraint of species flow though the community establishes a set of mutualistic relationships among a subset of species in a given cell. In species competition, and those species that are linked, have an extinction probability equal to the lowest extinction probability among the linked species.
disperse_species	Disperses species among adjacent cells based on probability of extinction among species inhabiting the cell.	In dispersal events the species with the lowest extinction probability is selected to spread from the cell. This constraint sorts the species, by extinction probability. If there is room for another species in a randomly chosen neighbor, the species is instantiated in the chosen cell. Note: it is not dispersal in the sense of an individual moving away from one cell and into another. Rather, a species becomes established in the new cell while the species continues to remain present in the cell of origin.
species_compete	Competition within a cell between a randomly chosen species that has mutualistic relationships with other species in the cell, and another	This constraint compares two species chosen at random, one with mutualistic

	randomly chosen species in the cell that does not have mutualistic relationships within the cell.	associations and the other without. The species with the highest probability of extinction goes extinct. This opens a space in the cell for another species to move into the cell from other processes such as dispersal or speciation.
speciate_without_species_drift	Species spread to a new opening in the cell with attributes derived from the mean value of the parental species' species_niche_function score and variation from that score defined by the parameter variation_in_extinction_probability from which the extinction probability of the new species is derived.	This constraint represents the spread of the species to an opening into an empty niche space within a cell. The species created from the parental species has the same mean value niche score as the parental species but with a given variance specified with a parameter given in column left. Species that can form mutualistic relationships remain able to form such relationships.
speciate_with_species_drift	*speciate_with_species_drift*, is identical to *speciate_without_species_drift* except it adds the possibility of species to drift from their trait-based functional group. This includes the possibility of networked species becoming non-networked species and vice-versa.	This constraint focuses the spread species to an opening into an empty niche space within a cell. The species created from the parental species has a potentially different mean value niche score as the parental species and with a given variance specified with the parameter given in

		column left. Species can change from being able to form mutualistic relationships to those who cannot, and vice versa.
cause_catastrophe	*cause_catastrophe* causes catastrophic ecological collapse at predefined intervals set by, *frequency_species_eco_perturbation*, and in intensity defined by *percent-species-to-wipeout*	This constraint causes random species loss without regard to their extinction probability. The species are selected for extinction with probability defined according the probability proportional the parameter in left column of percent species affected. These events happen periodically set with a parameter randomly selected prior to initiation of the model.

Table 3: Evolutionary and ecological processes thought to constrain the flow of species through an ecosystem.

Parameter name	**Parameter type and units**	**Parameter meaning**
spatial_habitat_patch_distribution_parameter_1	Integer, range [1, 20]	Sets the spatial distribution and patch structure of model, including density, and permeability of cells at landscape level.
maximum_time_to_run	Integer, range [1, 100,00]	Number of time steps to run model.
percent_species_loss_eco_perturbation	Real random variable, range [0, 100]	The number of species lost in a cell due to ecology perturbation without regard to extinction probability.
frequency_species_eco_perturbation	Integer random variable, range [0, 10,000]	Time steps between ecological perturbations.
maximum_number_speices_per_patch	Integer, range [5, 100]	The number of species occupying the packed niche space of the cell.
number_linked_species_per_patch	Integer, range [2, 100]	The number of linked species possible.
maximum_intial_proportion_links	Real, range [0.01, 0.99]	The initial proportion of linked species, out of total maximum linked species, present in the patch.
variation_in_extinction_probability	Real random variable, range [0, 0.25]	When a new species is spawned from an old, the variation in extinction probability from parental species.
species_drift_variation_speciation	Real random variable, range [0, 0.1]	The variation between parental species and new speciation in functional group of parental species.

Table 4: Global parameters initialized at the beginning of the model (all random variables are drawn from a uniform distribution).

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Appendix 1: Supplementary Information S1: ODD

This model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm, et al. 2006), as updated by (Grimm, et al. 2020). A copy of the peer-reviewed model code can be found at Steve L. Peck (2020, December 06). "Evolution of Ecological Communities: Testing Constraint Closure" (Version 1.0.0). CoMSES Computational Model Library, and can be retrieved from https://www.comses.net/codebases/c9d55182-4444-4cc1-9a6f-dcf9c4ca942a/releases/1.0.0/.

1. Purpose and patterns

The following theoretical model has been designed to provide in principle arguments for how constraint closure of evolutionary dynamics may provide ecosystem stability in the sense described by Moreno and Mossio (Moreno and Mossio 2015). We explore this using a set of Mark Vellend's proposed processes for conceptually framing evolutionary changes in a set of species comprising the niche structure of ecological communities. In particular, the model includes Vellend's suggested processes, selection, species-drift, speciation, and dispersal (Vellend 2016), as well as ecological perturbation and mutualism. We hypothesize that these will allow several patterns of standard measures of ecological stability to emerge as a result of constraint closure. We argue that evolutionary dynamics acting on the flow of species through an ecosystem can be considered constraints, in which closed loops providing constraint closure emerge. In this model, we suggest that these processes act in such a way that the semi-autonomy of the ecological community emerges, creating conditions of stability. Specifically, we expect the model to show increases in stability measures as the number of constraints increases, especially as the number of constraints moves beyond the three proposed necessary to achieve constraint closure. The model is written in NetLogo 6.0.2 an Agent-Based Programming Environment, (Wilensky 1999).

2. Entities, state variables, and scales

Following Vellend's work, the model comprises two types of entities, species (rather than individual organisms), and grid cells that do not represent a physical metric space but a space of fixed ecological niches. Species compete within grid cells, send lines of descendants to adjacent grid cells, and can go extinct. The entities in the model include species representing the inhabitants of an ecological community. Grid cells represent spatially adjacent ecological niches, and a global environment representing a landscape comprised of inhabitable and uninhabitable locations.

2.1 State variables: species (agent)

Rationale: Species are the only agent in the model. The state variables for species are given in Table 1. Each species has a state variable called *species_preferred_niche_score*, which represents a one-dimensional measure of the species' resource needs. This variable corresponds to the cell state variable, *cell_niche_score*, which in turn is a measure of what needs that habitat will provide. A species' extinction probability will be defined as the absolute difference between these two variables.

Each of the species in the model belongs to a functional group located in each cell defined by the species state variable *species_niche_function*. This variable defines a trait-based functional group that the species plays in the community (e.g. in a real ecosystem, these might be such ecological functions as predator, herbaceous plant, etc., in the model the functional group is defined as an integer value that characterizes a set of traits with a single value), and different species can be in the same functional group. This trait-based functional group can change by wandering randomly through species-drift. Cells may be completely homogeneous or contain the entire gamut of possible ecological functional groups that a species can take on in the model. Because the number of species in a cell is fixed, is variable serves as a surrogate for differences in species in ecological evenness measures.

A subset of the species in the model may form mutualistic relationships with other species that can affect the extinction risk of the species involved.

Species can send lines of descent into adjacent cells in which the niche is not completely packed with species, and there is room among the niches for another species. Species are in competition with others in a given cell regardless of linked or unlinked status. They can also undergo catastrophic ecological collapse, species selection, species-drift, and other processes discussed in (Vellend 2016).

2.2. State variables: cells

Rationale: All of the state variables of the cells are given in Table 2. The unsuitable habitat cells are places where species cannot exist and form a barrier or impediment to migration. Each habitat cell represents a packed set of niches that can hold a given number of species representing *maximum_number_speices_per_patch* ecological functional trait groups in the niches of the cell. Each cell contains an environmental variable, called *cell_niche_score*, which a habitat suitability index is chosen from a uniform random distribution between 0 and 1.

2.3 Spatial and temporal scales

Rationale: The space represented in the cell is non-Euclidean and space is only defined in terms of adjacency, i.e., cells may be near or far from each other, but there is no measure of distance *x* between cells. Each cell represents a fixed number of possible species viewed as functional groups. Time is specifically modeled, and each time step represents the mean time any species is likely to exist in a community before cell extinction or species evolution. The model is structured on a 16x16 (although much larger grid sizes, this captured the basic dynamics and was used for the exploration of the parameter space) spatial toroidal grid composed of cells that form clusters of suitable and unsuitable areas. The procedure for setting up the topological aspects of the grid is based on O'Sullivan and Perry (O'Sullivan and Perry 2013).

3. Process overview and scheduling

After establishing the world's initialization (details below), the following processes take place in the following order.

3.1 Module: create_species_networks
. **Brief Description**: This creates the linkages that will serve as mutualistic relationships among species. This creates formal links among subsets of species within a cell which will influence the fitness relationships of those species able to form such links.

3.2 Module: disperse_species. **Brief Description**: Species dispersal copies the species with the lowest extinction probability and moves the new instantiation to an adjacent cell if there is room for a new species. In the new cell, new extinction probabilities are calculated and join the network if it is a species able to form mutualistic relationships. In this way, species send descendants into adjacent cells in which there is room to hold another species. They can also undergo catastrophic ecological collapse, species selection, species-drift, and other processes discussed in (Vellend 2016).

3.3 Module: Species _compete. **Brief Description**: Competition among networked and non-networked species. A random species is chosen from networked and non-networked species, respectively. The species with the lower extinction probability goes extinct (note: in the competition between the species chosen, there is no advantage to being networked), and the winner speciates. Either (4a) or (4b) is executed depending on the initialization choices.

3.4.1 Module: speciate_without_species_drift. **Brief Description**: Speciation without drift New species are created from the parental species. No possibility of species-drift.

3.4.2 speciate, with_species_drift. **Brief Description**: Speciation with drift New species are created from the parental species. Possibility of species-drift.

3.5 Module: cause_catastrophe. **Brief Description**: Periodic ecological perturbation Periodic ecological perturbation at given intervals that causes the local extinction of a proportion of the species in a cell without regard to extinction probabilities.

3.6 Module: *select_with_drift_species_w_lowest_exinction_probability*. **Brief description:** Extinction of species In each cell (randomly examined), all of the species' *probability_of_species_extinction* is calculated as the absolute value of the difference between the *species_preferred_niche_score* and the cell's *cell_niche_score.* An undirected network is established between species in a subset of species chosen at initialization. The extinction probability of a linked species differs from unlinked species in that its demise in various places in the model is calculated as the lowest extinction probability of all the linked species considered as a collective. In species that are networked, the probability of extinction is the lowest probability of extinction among the set of all of the networked species. The species with the highest extinction probability goes extinct.

4. Design Concepts

4.1 Basic Principles

This agent-based theoretical model explores whether basic evolutionary processes found in ecological communities can form constraint closure in a way that creates ecological community stability. By using the ideas of constraint closure, we hope to provide a theoretical proof of concept for some of the patterns found in such communities and offer plausible interpretations of such patterns. The following is a generalized model. We are not trying to target a specific ecosystem found in a field study reported in the scientific literature but rather to keep an eye toward the kind of interactions found in the broad class of community systems. To put the following in terms of the model mapping schema provided by Weisberg (2013) (Weisberg 2013) the model below is a generalized, agent-based computational model, using a minimalist idealization of key processes thought to potentially function in ecological communities, i.e., evolutionary dynamics such as selection, species-drift, speciation, and dispersal. In addition, including elements common to ecological communities such as mutualism, and in addition, perturbations that indiscriminately affect species in an ecosystem (e.g., fires, hurricanes, and habitat destruction by human activity). The model considers the kind of constraints thought to capture the dynamics that confer biological autonomy and stability. These two ideas should allow community stability, as recognized by signature patterns to emerge. The fidelity criteria we aim for will be achieved if such patterns are present and suggest that these processes are sufficient to confer known emergent attributes to these model systems.

4.2 Emergence

We expect emergence to occur in two ways. In the first, we expect the evolutionary processes encoded in the model that affect species flow through the cells to emerge in the model as constraints. Second, we expect ecological stability to emerge as certain combinations of constraints form a closed loop of interaction and create constraint closure among the ecological processes described above.

4.3 Collectives

Mutualism among species in the model is explicitly included as one of the ecological processes considered as a possible constraint on species flow. Some of the species have the ability to form networks that lower the extinction probability of all species in a collective. The collective in effect has a lower extinction probability than those not in the collective.

4.4 Adaptation

Species that form networks compete with those that do not. Species are replaced each time step with instantiations of new species with the same mean niche score as the parental species within some variance determined by the difference between the cell's resource score and the species resource needs score. At each time step, species with the highest extinction probability go extinct, creating room for species with lower extinction probabilities to replace them through dispersal, speciation, or competition.

4.5 Sensing

The observer can sense if a cell in the adjacent eight cells has room for another species.

4.6 Interaction

Species within a cell compete as individual species.

4.7 Stochasticity

Stochasticity enters into the model in several places: (a) the initial cell structure of the landscape is randomly generated; (b) the proportion of species chosen to form links is a random variable; (c) the species that go extinct in the drift stage are randomly chosen with probability proportional to fitness; species with the lowest probability of extinction are chosen to move, and then move randomly to one of their 8-Moore-neighborhood neighbors; (d) the variation in fitness around newly formed species is a random variable.

4.8 Observation

Testing: The module BehaviorSpace in NetLogo 6.0.2 was used to test the overall behavior of the model, in a Latin hypersphere run of the model with random non-constraint independent variables. The following analyses were used to reconstruct the effects of the constraints on the model landscape. Much larger grid sizes were tested to find the minimal size needed for running a complete iteration set of the binary switches turning on and off the constraint *submodels* and for three values of the possible number of links per species, and two values of each of the parameter values given types given in Table 3. leading to 256 possible combinations that compromise the permutation set used to explore the constraint space, with 500 timesteps for each sample from the model hyperspace. A uniform random distribution of the variables found in Table 4, were drawn from the 2000 replications of each of the possible constraint permutation sets for each of the runs. These were sampled with replacement over the multidimensional parameter space. As White et al. (2014) note (White, et al. 2014), these results should not be interpreted as a test of statistical significance of parameter differences as the likelihood values, and statistical tests, are easily influenced by the number of iterations used in the model testing. Therefore, p-values were provided only as a heuristic.

4.9 The following variables were used to assess the patterns found in the model:

4.9.1 Evenness: Evenness was measured using a modified Pielou's evenness index. It was modified for algorithmic efficiency. Rather than the mathematical equation, $J' = \frac{H'}{H'_{max}}$ where H' is Shannon's Index, $H' = -\sum_{i=1}^{S} \frac{p_i}{\ln p_i}$, where p_i is the proportion of the i^{th} species, and S is the maximum number of species, we modify it as follows: Because the number of species per cell is fixed, the algorithm used is computed by the number of unique functional morpho-species in a cell, divided by the number of species in the cell. This has the range $\left[\frac{1}{S}, 1\right]$, where the lower range is found in the case where every species in the cell is functionally unique, and the higher when there is only one species type.

4.9.2 Turnover rate: Turnover is modeled such that new species arise when there is an opening in relation to the packed niches of each cell. This opening occurs in two places: (1) when there is selection between the linked and unlinked species in which the least fit species is eliminated; and (2) in perturbation events when a large number of species go extinct without regard to their fitness status as might happen in a large natural disaster such as a wildfire.

Functional species groups: Because the number of species in a cell is fixed, the richness used in the model defines the number of functional types present. Therefore, species of a unique type, rather than species, as such. For example, if the cells have only one kind of species, the richness as defined here would be 1.

4.9.3 Landscape fitness: This is the mean extinction probability of a species averaged over all inhabitable cells. It is expected that this will increase over time as the species better aligns with the cell niche score.

5. Initialization

5.1 Cells

Cells are set up as being a random grid of suitable habitat, in which species can exist, or unsuitable habitat, which serves as an uninhabitable matrix and a barrier to migration or movement, Fig. 2. A landscape parameter, *spatial_habitat_patch_distribution_parameter_1*, is used to determine the landscape of cell features such as permeability, how the habitat cells are clustered, and other macroscale features of the landscape cell distribution. Each cell is given a niche attribute, *cell_niche_score*, with which species will be compared on their, *species_preferred_niche_score*. Their closeness to this value will determine their extinction probability in the cell. Cells are initialized to have the maximum number of species they can hold, representing packed niches.

5.2 Species

Species are initialized on a habitat cell with a random location on the matrix of cells, and a niche score, *species_preferred_niche_score*, that will be compared with the niche score of the habitat cell, *cell_niche_score*, on which they land is used to calculate the extinction probability. They are also assigned a functional trait group, *species_trait_group*, a score that will be used to determine its fit to the ecosystem defined in a cell. The functional group is used to separate the species. These functional types are not meant to represent actual species but are designed to mirror the idea of trait-based functional groups. Networks of linked species are established.

5. 3 Model Initialization Parameters

For the model runs, several parameters are set that will be used throughout the simulation detailed in the *submodels* found below. A complete list of these is given in Table 3.

6. Submodels

6.1 create_species_networks

create_species_networks works on individual species. First, it looks to see whether there are any species present in the cell. Then, it establishes directed links with those species with a species number less than the *number_linked_species*_per_patch variable. The species first receives a species number sequentially at first. Therefore, this forms links only for those whose species number is less than the number that can form links. Cells can be composed of completely linkable species or non-linkable species depending on the evolutionary dynamics that play out elsewhere in the model.

Algorithm for submodule

Uses link set: mutualisms

1. For each species in the cell, if any are present;
2. form a set of all species that are eligible to form an undirected linked network
3. calculate the number of links to create as *maximum_number_of_links* * *maximum_intial_proportion_links*
4. create the given number of links from step #3 among the identified eligible species

6.2 create_little_network

Operates identically as described above, but used for a single species newly created or migrating from another cell.

6.3 select_species_with_lowest_prob_extinction,

select_species_with_highest_prob_extinction, first sets the probability of extinction as the given species to the lowest probability of extinction of those species it has a link with (so that being in a network increases the fitness advantage of the entire network). It then causes the extinction of the species with the lowest fitness.

Algorithm for submodule

1. For all linked species in a cell
2. Change the probability of extinction to the lowest probability among those species with which it is linked.
3. Sort by probability of extinction from high to low.
4. Cause the extinction of the species with the highest probability of extinction.

6.4 ***disperse_species***

disperse_species, sorts the species by extinction probability within a cell, and checks the existence conditions that appropriate species are present in the cell. It then takes the species with the lowest extinction probability, hatches a new species and then moves it to an adjacent habitable cell with room for a new species, lets the species establish mutualisms with their new neighbors, and recalculate its extinction probability. The "else" segment moves species without links to the new cell and calculates its new fitness in the new cell. It hatches a new species first, then looks for room, then moves there, or it goes extinct.

Algorithm for submodule

Within a cell
1. Find the species with the lowest extinction probability
2. Create an new instance of that species
3. Randomly search the adjacent cells to see if there is room for another species
4. If so, move species to that cell
    (a) If it is a species able to form a network establish network in a new cell
    (b) Establish its extinction probability in the new cell
5. Else if there is nowhere to go, cause the extinction of new instantiation of species

6.5 species_compete

species_compete picks one of the linked species and one of the unlinked species and compares the two. The winner of the contest speciates, while the loser dies. This function also allows the possibility of species-drift.

Algorithm for submodule

Within a cell
1. Pick one species randomly from the linked species and one from the unlinked species.
2. Pick a competitive winner by comparing the two species' probability of extinction and choosing the one with the highest extinction probability.
3. Speciate with or without species-drift (set by initialization parameter).
4. Cause cell extinction in the non-winning species.

6.6 Specate _without_species_drift

speciate_without_species_drift is an algorithm designed to create a speciation event such that the new species has the same attributes as the parental species, but with some variation. It takes a species and creates a new species based on the parental species mean extinction probability and adds variation, *variation_in_extinction_probability*, which is set at initiation. For those species with links, it creates links with create-little-network.

Algorithm for submodule

1. For each species targeted for speciation—
2. Add or subtract random variation from its extinction probability based on a random variate from the variable, *variation_in_extinction_probability*.
3. Check it is not < 1 or > 0
4. If it is, reflect back the amount remaining above or below the boundary
5. Create a new instantiation of that species
6. Set its extinction probability to the calculated value

6.7 speciate_with_species_drift

speciate_with_species_drift is identical to *speciate_without_species_drift*, except that it adds the possibility of species to drift from their functional group. This includes the possibility of networked species becoming non-networked species and vice-versa.

Algorithm for submodule

1. The algorithm of this submodule is identical to steps 1-6 of the algorithm in *speciate_without_species_drift.*
2. With equal probability increase or decrease the *species_trait_group* by one.
3. Check it is not over or under the allowable boundaries
4. If it goes outside of the boundaries, reflect back the increase or decrease.

6.8 cause_catastrophe

cause_catastrophe causes catastrophic ecological collapse at predefined intervals defined by, *frequency_species_eco_perturbation*, and in intensity defined by *percent-species-to-wipeout*.

1. At time interval mod(*frequency_species_eco_perturbation) = 0*
2. In all cells
3. Loop through all species
4. Cause a species to go extinct with probability *percent-species-to-wipeout*

Appendix 2: Supplementary Information S2: Influence of evolutionary and ecological processes that emerge act constraints on model outcomes

Fig. S1. *Average community fitness across parameter space for all possible combinations of constraints.* See the ODD in supplemental information S1 for more details. This figure provides a closer look at the processes analyzed in the main body of the article and described in Fig. 5 of the paper. Fitness is defined in the model as the extinction probability ($prob(extinction)$). Lower values of extinction probability imply higher fitness. This figure provides specific information on how each of the evolutionary and ecological processes individually and in interaction, with all other represented constraints, affect the simulated landscape representing a community of species. The figure shows the effect of constraints on average community fitness across all combinations of the model's parameter space. As the number of constraints increases, the overall pattern the most influential evolutionary processes in interaction with the others can be examined. For example, when $number\ constraints = 0 \Rightarrow prob(extinction) > .3$ which serves as a baseline fitness with which to compare how adding constraints and their interaction affect average fitness levels of species in the simulated community. When the model is run with $number\ of\ constraints = 1$ the evolutionary processes representing *selection* and *competition* increase fitness more than other processes ($Prob(exiinction) < 0.1$) for both processes. This is not unexpected as these are evolutionary forces known to influence fitness strongly. Of special note is when there are three constraints present, 16 of the 20 possible interactions show a high fitness, with the $extinction\, probility < 1.3$ implying that when $number\ contraints \geq 3$ there is a pattern of higher average landscape fitness in the digital ecology of the simulated community than when there are fewer constraints.

Fig. S2 *Average ecological evenness across parameter space for all possible combinations of constraints.* See the ODD in supplemental information S1 for more details on how ecological evenness is defined. This figure provides a closer look at the processes analyzed in the main body of the article and described in Fig. 6 of the paper. This figure provides specific information on how each of the evolutionary and ecological processes individually and in interaction with all other represented constraints affect the simulated landscape representing a community of interacting species. The figure shows the effect of constraints on average community evenness across all combinations of the model's parameter space. As the number of constraints increases, the overall pattern of the most influential evolutionary processes in interaction with the others can be examined. For example, when $number\ constraints = 0 \Rightarrow average\ ecology\ eveness > .7$ which serves as a baseline evenness with which to compare how adding constraints and their interaction affect average fitness levels of species in the simulated community. When the model is run with $number\ of\ constraints = 1$ the evolutionary processes representing *selection* and *competition* increase evenness more than other processes ($average\ ecology\ eveness < 0.2$) and for the process ecological catastrophe ($average\ ecology\ eveness < 0.3$). Of special note is when there are two constraints present, 7 out of 15 interactions average ecological evenness < 0.2 and for three interactions, 8 of the 20 possible interactions show ($average\ ecology\ eveness < 0.2$), with the average ecological evenness increasing for higher parameter values. This suggests greater diversity but not so high that only unique individual species occur in each cell and away from very low diversity being present in a cell for higher values of ecological evenness. Recall from the ODD found in that

This has the range, $\left[\frac{1}{S}, 1\right]$, where S is the number of unique functional group in which the lower range is found in the case where every species in the cell is functionally unique, and the higher when there is only one species type. This shows that the model itself because of the structure of the simulated community special components does not allow the theoretical maximum to occur, which should be taken into account when evaluating the meaning of the evenness achieved for the various constraint numbers and interactions.

Fig. S3. *Average ecological richness as defined by number of functional groups present in a cell across parameter space for all possible combinations of constraints.* See the ODD in supplemental information S1 for more details on how richness is defined and calculated. This figure provides a closer look at the processes analyzed in in the main body of the article and described in Fig. 7 of the paper. It provides specific information on how each of the evolutionary and ecological processes individually and in interaction with all other represented constraints affect the simulated landscape representing a community of interacting species. The plots show the effect of constraints on the average of the cell species' richness across all combinations of the model's parameter space. The is at a maximum when there are no constraints when $number\ constraints = 0 \Rightarrow average\ richness > 15$ with which to compare how adding constraints and their interaction affect average fitness levels of species in the simulated community. When the model is run with $number\ of\ constraints = 1$ the evolutionary processes representing *selection* and *competition* restrict the richness severely (while noting from Fig. 8, in the main article the number of constraints does not impact the overall community variance in richness so depauperate individual cells do not imply a less rich community just less within cell richness). the average richness of these two processes ($average\ richness < 5$) and for the process ecological catastrophe which also reduced cell richness ($average\ richness < 10$). Of special note is when there are two constraints present, 7 out of 15 interactions average richness < 5 and for three interactions, 8 of the 20 possible interactions show ($average\ richness < 5$), with the average richness increasing for some of the constraints including those with the two most relevant to species richness reduction. However, the propensity for species to rebound to greater richness even in the presence of *selection* and *competition* suggests that even after three constraints, a greater number of interactions are increasing in richness. This increase in richness continues as constraints are added despite evolutionary and ecological forces that reduce richness in individual cells.

Appendix 3: Organizational approach (OA) to ecological communities and persistence enhancing functions (PEP)

Mossio, Saborido, and Moreno (Mossio, et al. 2009) formally define biological function as, "A trait T has a function in the organization O of a system S if and only if:

- C1 : T contributes to the maintenance of the organization O of S;
- C2 : T is produced and maintained under some constraints exerted by O;
- C3 : S is organizationally differentiated." p. 828

This is in contrast to the Etiological Approach (EA), which uses evolutionary history to define function as doing that which it was selected to do in an adaptationist sense. OA then considers only what the function does in the current ecosystem, not as it is embedded in its historical or evolutionary framing. This, drawing on the work of Moreno and Mossio (Moreno and Mossio 2015) on constraint closure, leads to an ecological definition of function, by Nunes et al.. An ecological function is a precise (differentiated) effect of a given constraining action on the flow of matter and energy (process) performed by a given item of biodiversity in an ecosystem closure of constraints " (Nunes-Neto, et al. 2014).(p. 131)

This provides a handle for seeing ecological communities as autonomous systems, as maintained by constraint closure. The constraints are modulations induced by the components of biodiversity acting on the flow of matter and energy through the system, such that they feed back into the maintenance of the ecosystem. It is important to point out that the claim of its being an autonomous system is not the same as the claim that they are individuals in the biological sense, although they do seem to exhibit weak individuality (Huneman 2011).

Dussault and Bouchard(Dussault and Bouchard 2016)add a significant consideration to the above account, developing a focus on particular kinds of functions that they call persistence enhancing propensities (PEP). PEPs are a class of functions that allow the currently structured ecosystem to persist. The focus is not on these functions in an adaptive sense, such that their historical grounding has been necessarily worked out. Rather, it is future-directed such that it attends to the extant functions that contributed to current stability--defined as the ability to return to equilibrium after a disturbance. They define a PEP function as

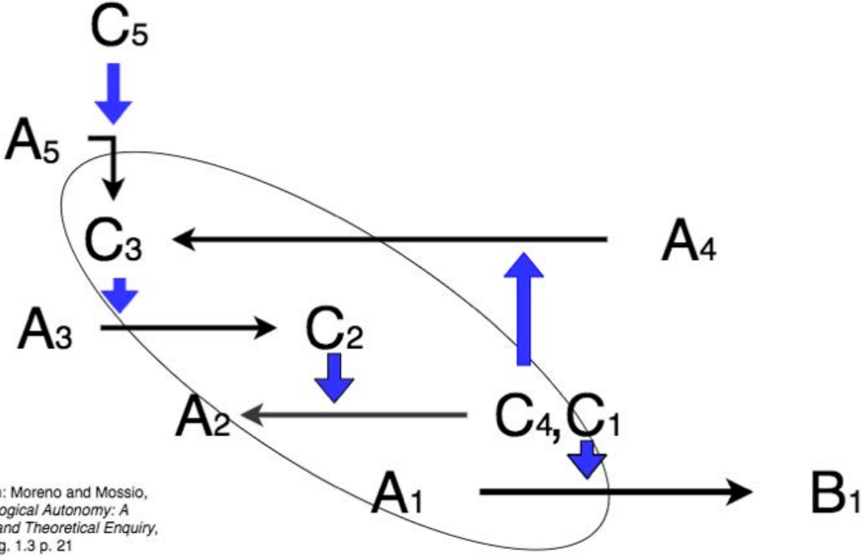
"The PEP function of x in an ecosystem E is to F if, and only if, x is capable of doing F and x's capacity to F contributes to E's propensity to persist." (Dussault and Bouchard 2016) p. 8)

PEPs then allow us to explore the question of what features provide for the ability of this ecosystem to survive disturbances to equilibrium. It pulls away from questions about how particular assemblages come to be constructed and looks for general characteristics of ecosystem functioning and construction that are based on the functional group that species play in the current community.

These two proposals (OA and PEP) offer possible connections with the evolutionary constraints we develop below regarding ecological communities and that influence stability and structure, which allow them to be considered autonomous systems.

Dussault, A. C. and Bouchard, F. 2016. A persistence enhancing propensity account of ecological function to explain ecosystem evolution. - Synthese: 1-31.
Grimm, V., et al. 2006. A standard protocol for describing individual-based and agent-based models. - Ecological modelling 198: 115-126.
Grimm, V., et al. 2020. The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. - Journal of Artificial Societies and Social Simulation 23.
Huneman, P. 2011. About the conceptual foundations of ecological engineering: Stability, individuality and values. - Procedia Environmental Sciences 9: 72-82.
Moreno, A. and Mossio, M. 2015. Biological Autonomy: A Philosophical and Theoretical Enquiry. - Springer Netherlands.
Mossio, M., et al. 2009. An organizational account of biological functions. - The British Journal for the Philosophy of Science 60: 813-841.
Nunes-Neto, N., et al. 2014. Function in ecology: an organizational approach. - Biology & Philosophy 29: 123-141.
O'Sullivan, D. and Perry, G. L. W. 2013. Spatial simulation: exploring pattern and process. - John Wiley.
Vellend, M. 2016. The Theory of Ecological Communities (MPB-57). - Princeton University Press.
Weisberg, M. 2013. Simulation and Similarity: Using Models to Understand the World. - OUP USA.
White, J. W., et al. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. - Oikos 123: 385--388.
Wilensky, U. 1999. Netlogo.

Fig. 1



Adapted from: Moreno and Mossio, 2015, *Biological Autonomy: A Philosophical and Theoretical Enquiry*, Fig. 1.3 p. 21

Fig. 2

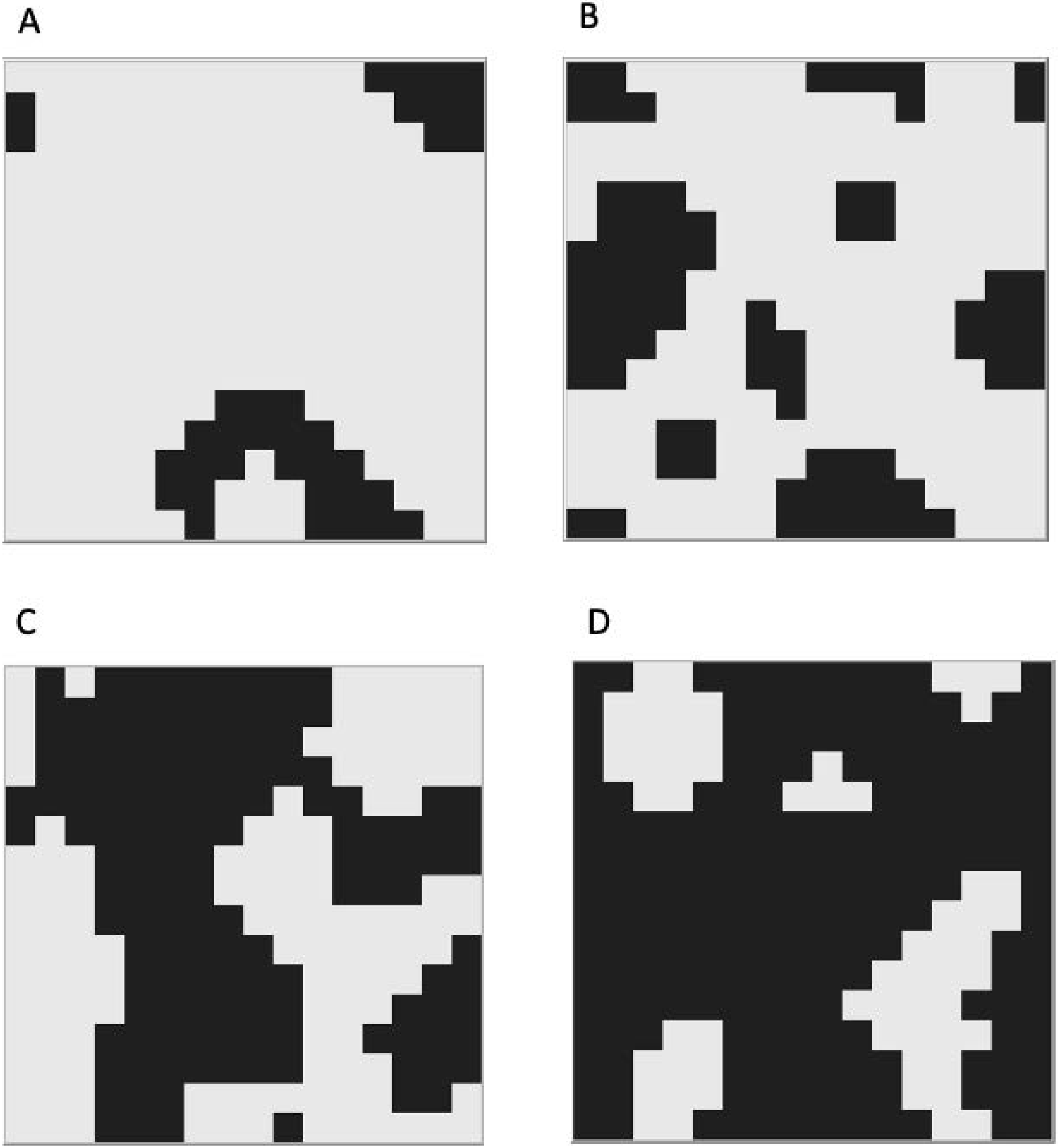
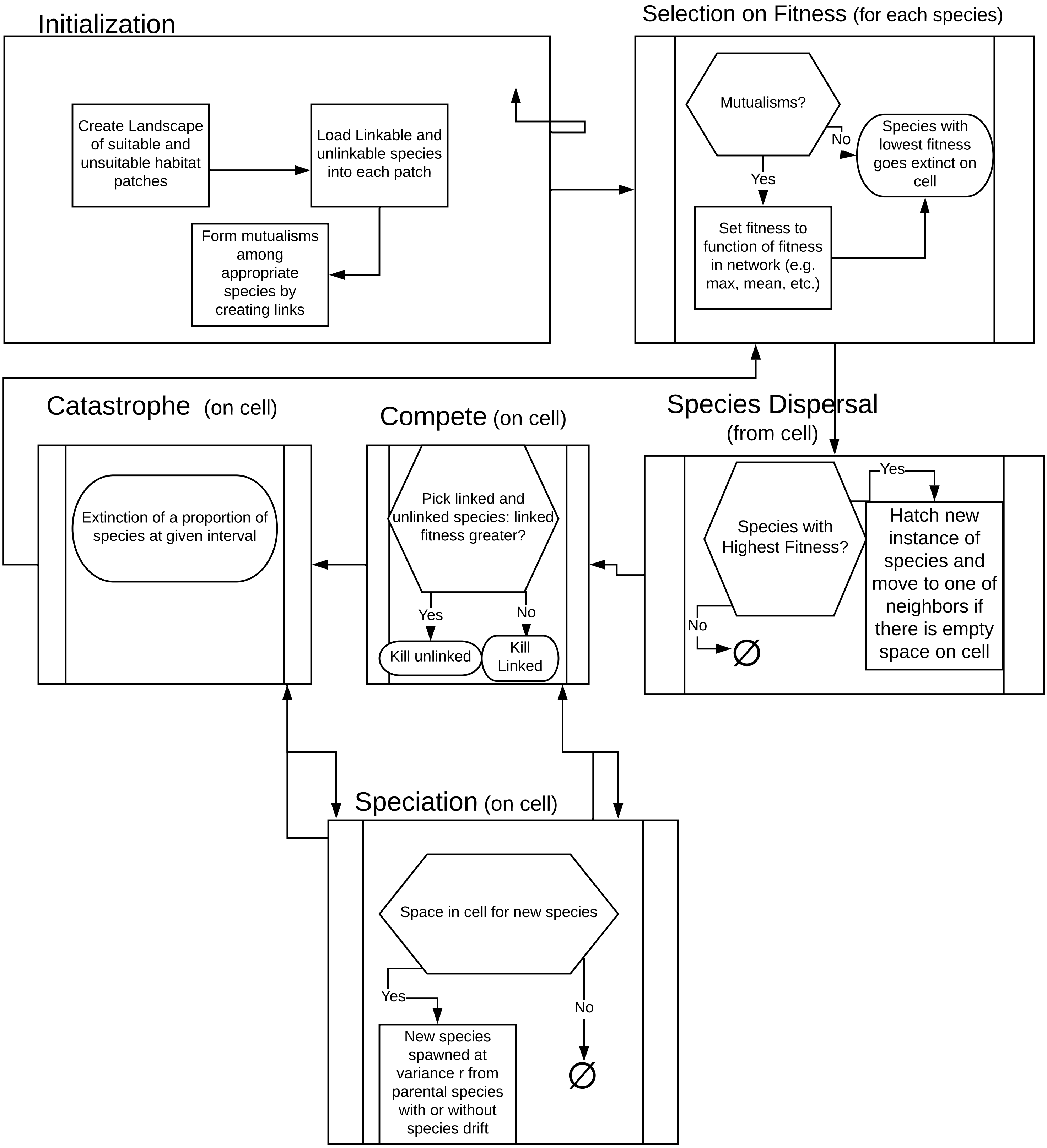
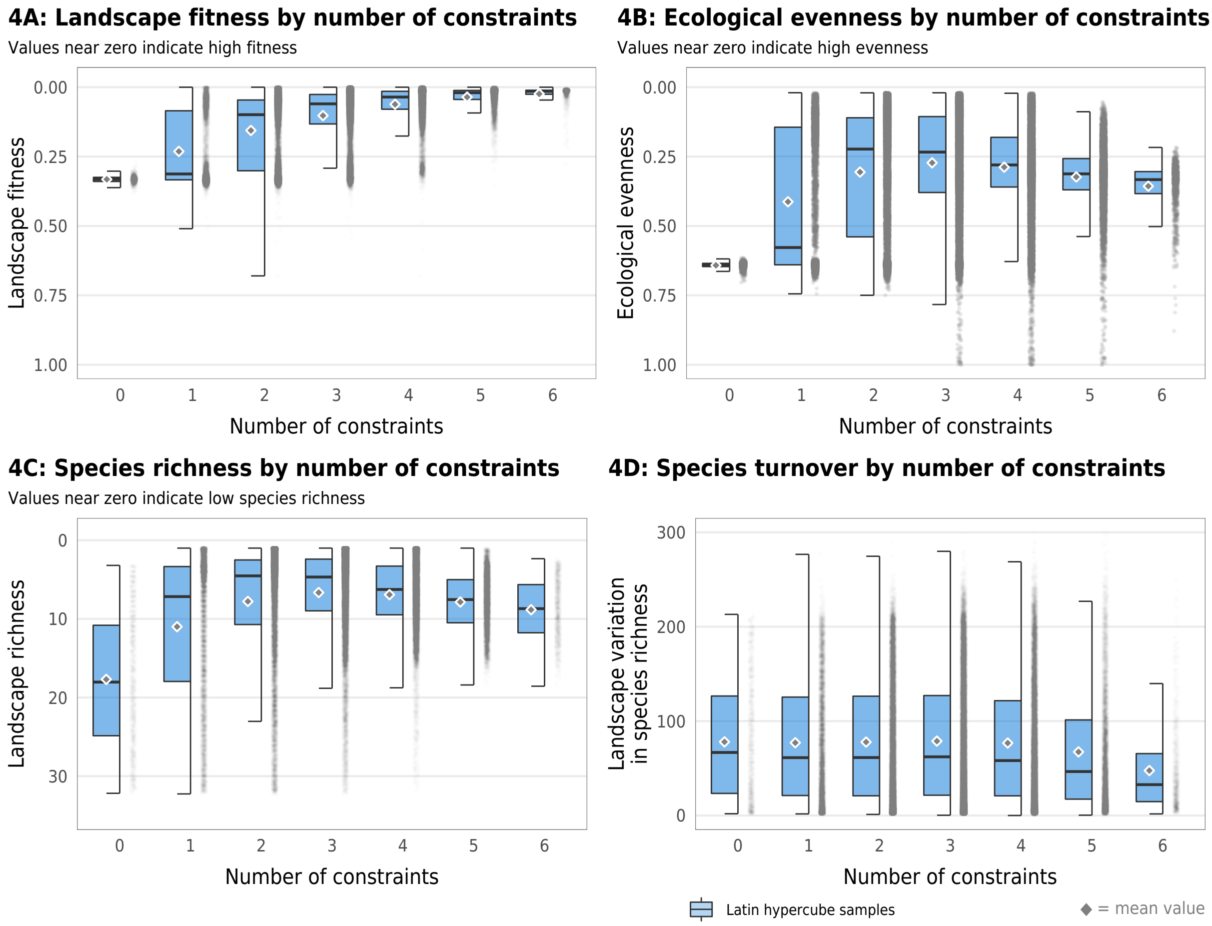


Fig. 3

Model Flow





4A: Landscape fitness by number of constraints

Values near zero indicate high fitness

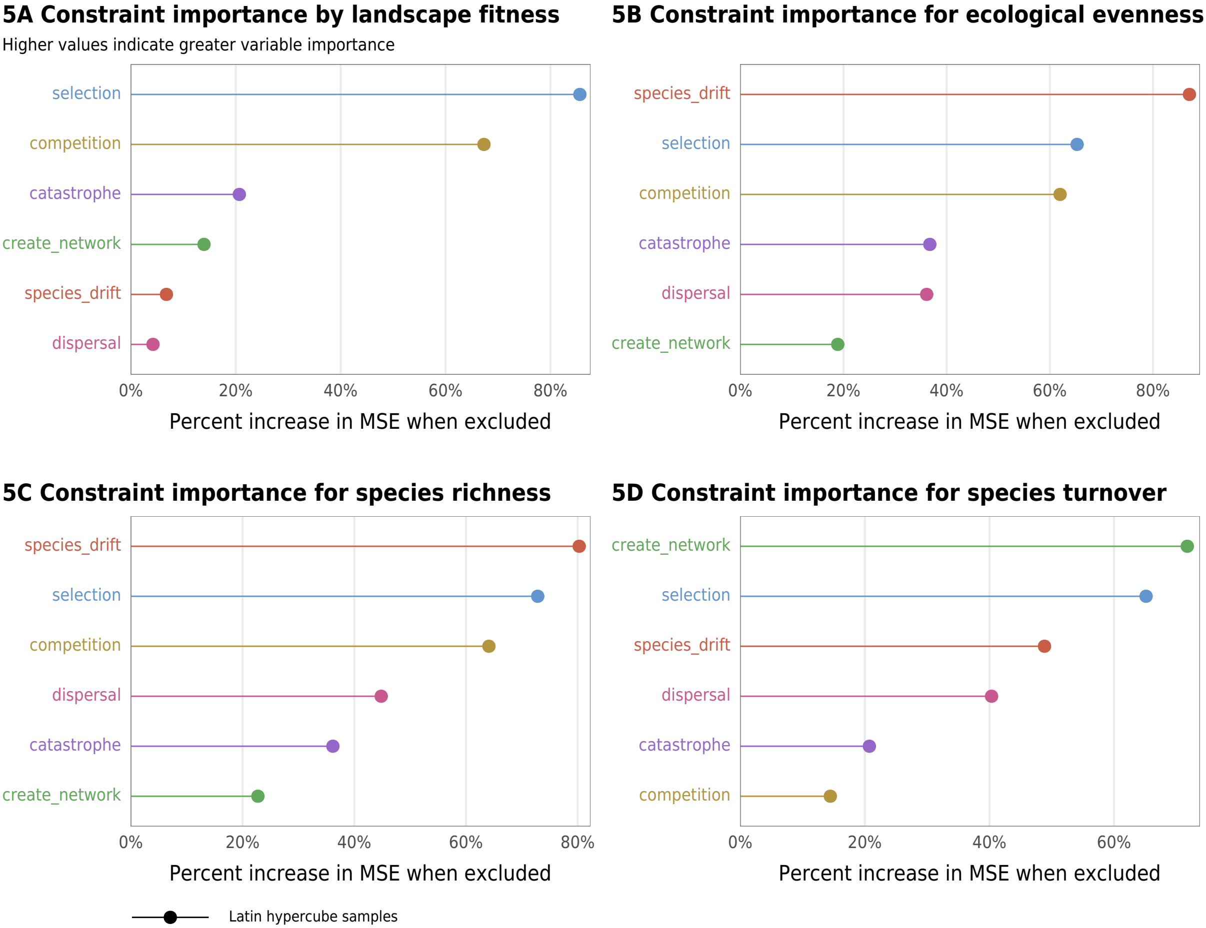
4B: Ecological evenness by number of constraints

Values near zero indicate high evenness

4C: Species richness by number of constraints

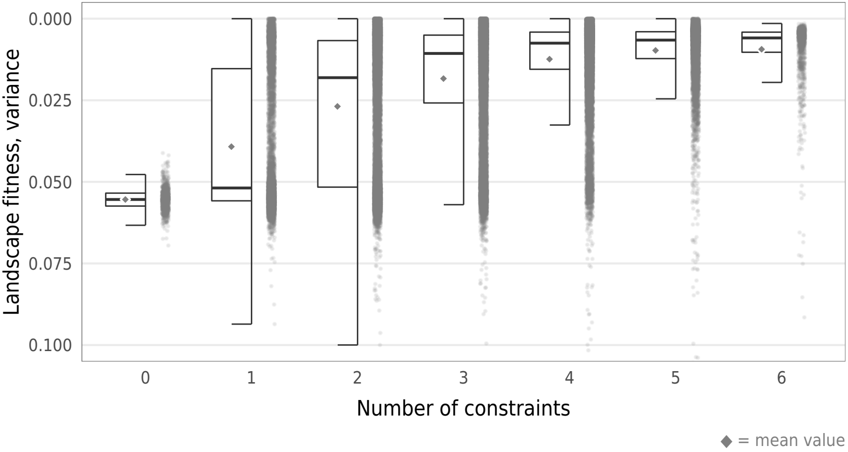
Values near zero indicate low species richness

4D: Species turnover by number of constraints


5A Constraint importance by landscape fitness
Higher values indicate greater variable importance
selection
competition
catastrophe
create_network
species_drift
dispersal
0%
20%
40%
60%
80%
Percent increase in MSE when excluded
5B Constraint importance for ecological evenness
species_drift
selection
competition
catastrophe
dispersal
create_network
0%
20%
40%
60%
80%
Percent increase in MSE when excluded
5C Constraint importance for species richness
species_drift
selection
competition
dispersal
catastrophe
create_network
0%
20%
40%
60%
80%
Percent increase in MSE when excluded
5D Constraint importance for species turnover
create_network
selection
species_drift
dispersal
catastrophe
competition
0%
20%
40%
60%
Percent increase in MSE when excluded
Latin hypercube samples

6: Variance in landscape fitness by number of constraints

Latin hypercube samples



7: Variance in speies richness by number of constraints

Turnover in linked species − turnover in unlinked species