The feasibility principle in community ecology

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Abstract

The structure and function of ecological communities are conceptualized as an emergent outcome derived from their corresponding set of interacting populations embedded in a given environmental context. However, it has remained unclear whether common principles can explain the biodiversity patterns that we observe across different contexts. Notably, finding general principles can successfully guide conservation and restoration efforts to minimize negative anthropogenic effects on biodiversity. To address this gap, I propose the *feasibility principle* in community ecology. Based on a compendium of theoretical work and empirical evidence on the feasibility of ecological communities, the proposed principle is based on three main postulates: (i) Ecological communities are feasible for a set of environmental contexts constrained by their internal structure. (ii) Self-organization leads to observable communities that are feasible for the largest set of local environmental contexts. (iii) Community transitions follow the path of least feasible changes within the environmental space. I summarize how the feasibility principle can be studied under a quantitative framework and contrasted with empirical data across a wide diversity of organisms and contexts. In the face of rapid climate change and habitat modification, I discuss how the feasibility principle can be used to assess the challenges and opportunities to mitigate biodiversity loss.

> *"For science, there are many possible worlds; but the interesting one is the world that exists and has already shown itself to be at work for a long time. Science attempts to confront the possible with the actual" François Jacob [1]*

A long-standing question in ecology is whether there are general principles that characterize the adaptability and evolvability of biological populations [2], regardless of the types of organisms and environmental contexts [3, 4, 5, 6, 7]. The existence of such potential principles can pave the way to increase our understanding of fundamental processes affecting the structure and function of high levels of living matter organization (e.g., biosphere) [8, 9, 10, 11]. For example, in community ecology [12, 13], the diversity within and across ecological communities is conceptualized as an emergent (i.e., non-reducible) outcome derived from the complex set of interacting populations embedded in a given environmental context [14, 15]. However, it has remained unclear whether common principles can explain the biodiversity patterns that we observe across different environmental contexts [16]. Notably, finding these general principles can successfully guide conservation and restoration efforts to minimize negative anthropogenic effects on biodiversity [17, 18].

To understand the biodiversity patterns of ecological communities across environmental contexts, I propose the *feasibility principle* in community ecology. This principle is rooted on a *structuralist perspective* [19, 20, 11], which postulates that changes in the state of a living system are catalyzed by external perturbations within an environmental space, but such effects are constrained by an internal structure of interactions among the components of the system as well as by the topology of the environmental space [2]. Following this premise, the proposed feasibility principle is based on three main postulates: (i) Ecological communities are feasible for a set of environmental contexts constrained by their internal structure. (ii) Self-organization leads to observable communities that are feasible for the largest set of local environmental contexts. (iii) Community transitions follow the path of least feasible environmental changes. Below, I summarize how the feasibility principle can be studied under a quantitative framework and contrasted with empirical data across a wide diversity of organisms and contexts. In the face of rapid climate change and habitat modification, I discuss how the feasibility principle can be used to assess the challenges and opportunities to mitigate biodiversity loss.

Quantitatively, feasibility has been formally conceptualized as the existence of a real and positive solution (e.g., positive population densities) under an ecological mathematical model, implying the *possible* long-term persistence of a system (pool of populations) $\mathcal{S}$ of n interacting populations [21, 22, 23, 24]. This possible persistence may or may not be dynamically stable (i.e, having the capacity to return to its equilibrium after a small perturbation in the population densities) [22, 25, 26, 27]. These models are typically of the form $\dot{N}_i = N_i f_i(\mathbf{N})$, where $\dot{N}_i$ is the time-derivative of population density N_i and the f's are multivariate polynomials in population densities $\mathbf{N} = (N_1, N_2, \ldots, N_n)^T$ denoting per capita growth rates [28]. Then, feasibility corresponds to the existence of at least one equilibrium point (i.e., $\dot{N}_i = 0 \ \forall i \in \mathcal{S}$), whose components (populations) are all real and positive (i.e., $\mathbf{N}^* = (N_1^*, N_2^*, \ldots, N_n^*)^T > \mathbf{0}$). If at least one of the components is not positive (i.e., at least one of the population densities is expected to go extinct in the long run), then the solution is called a boundary equilibrium (e.g., $\mathbf{N}^* = (N_1^* > 0, \ldots, N_{n-1}^* > 0, N_n^* = 0)^T$). By allowing boundary equilibria, it becomes then possible to talk about the feasibility of a given subset (community) of populations $\mathcal{C} \subseteq \mathcal{S}$.

Traditionally, feasibility conditions (typically represented by inequalities as a function of model parameters) have been attained by finding the isocline equations $f_i(\mathbf{N}^*) = 0 \ \forall i \in \mathcal{S}$ and then solving for $\mathbf{N}^*$ before finding the conditions that satisfy $\mathbf{N}^* > \mathbf{0}$ (i.e., imposing positivity) [21, 22, 29]. One of the most tractable models is the well known generalized Lotka-Volterra (gLV) model [3, 4, 30, 21], which describes the time evolution of population densities in a given system $\mathcal{S}$ based on a set of ordinary differential equations (in matrix notation): $\dot{\mathbf{N}} = \text{diag}(\mathbf{N})(\mathbf{r} + \mathbf{A} \cdot \mathbf{N})$, where $\dot{\mathbf{N}} = \{\dot{N}_i\}$ is the time-derivative vector of population densities, $\mathbf{r} = \{r_i\}$ is the vector of *effective* growth rates, and $\mathbf{A} = \{a_{ij}\} \in \mathbb{R}^{n \times n}$ is the pairwise interaction matrix denoting the mean per capita effect of population j on the growth rate of population i. The *effective* growth rate depicts, at a phenomenological, the net effect of the environment on the potential growth of a population. A negative r_i represents a net growth deficit (population i requires more energy that it can obtain in the absence of any other explicit population $j \neq i$ in system $\mathcal{S}$), such as a consumer population [31, 32]. In contrast, a positive r_i represents a net growth surplus, such as in a producer population [31, 32]. In turn, the interaction matrix $\mathbf{A}$ represents the explicitly considered bioenergetic transformations (typically observed as mass conservation) within system $\mathcal{S}$. This implies that the effective growth rate specifies the growth of a population as a function of its intrinsic properties and both the abiotic and biotic factors not explicitly considered in the interaction matrix $\mathbf{A}$. Notably, the gLV model can be derived from thermodynamics principles, from principles of conservation of mass and energy, and from chemical kinetics in large populations [3, 33, 34, 35].

The equilibrium solution ($\dot{\mathbf{N}} = 0$) of the gLV model can be written as the linear function $\mathbf{N}^* = -\mathbf{A}^{-1} \cdot \mathbf{r}$. Thus, by integrating a structuralist perspective under the gLV framework, we can assume that community changes in ecological systems (i.e., whether $N_i^* > 0$ or $N_i^* = 0$) are generated by different environmental factors (represented by different directions of the vector $\mathbf{r}$) constrained by an internal structure of such systems (i.e., the interaction matrix $\mathbf{A}$). Note that each direction of the vector $\mathbf{r}$ corresponds to a different relationship (or distribution) of effective growth rates among populations. This implies that the direction of $\mathbf{r}$, rather than its magnitude, is the main modulator of feasibility given a system characterized by $\mathbf{A}$ under the gLV framework [36, 37, 38]. Empirically, the interaction matrix $\mathbf{A}$ can be approximated from observational or experimental data under different assumptions [39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50].

The first postulate of the proposed feasibility principle states that a community $\mathcal{C} \subseteq \mathcal{S}$ is feasible for a set of environmental contexts constrained by its internal structure (Fig. 1). In other words, the first postulate implies that there is a possible world (regardless of whether it may only be a theoretical world) in which a community $\mathcal{C}$ is feasible. This first postulate can be formalized by the range of directions (regardless of whether they can be experienced by a community or not) in $\mathbf{r}$ (the environmental context) that are compatible with the feasibility of a community characterized by an interaction matrix $\mathbf{A}$ (the internal structure). Note that this assignment is based on mathematical convenience, and in theory, any parameter can be interpreted as context or structure [50]. Specifically, under the gLV framework, there is a one-to-one mapping between the solutions of a system $\mathbf{N}^*$ and the particular parameter values of $\boldsymbol{r}$ (i.e., $\mathbf{N}^* = -\mathbf{A}^{-1} \cdot \mathbf{r}$ or $\mathbf{r} = -\mathbf{A} \cdot \mathbf{N}^*$) [51, 45, 52]. That is, for a given ecological system $\mathcal{S}$ (pool of populations) characterized by interaction matrix $\mathbf{A}$, it is possible to find a set of directions in $\mathbf{r}$ that satisfies positive solutions (including boundary equilibria) for each of the 2^n subsets $\mathcal{C} \subseteq \mathcal{S}$ of possible communities, where a population from system $\mathcal{S}$ is either present or not [39, 53]. This compatible range of environmental contexts $D(\mathcal{C}, \mathcal{S}, \mathbf{A})$ is typically known as the *feasibility domain* of a community $\mathcal{C}$ within a system $\mathcal{S}$ constrained by interaction matrix $\mathbf{A}$ [34, 45, 54].

The second postulate of the feasibility principle states that self-organization leads to observable communities that are feasible for the largest set of local environmental contexts (Fig. 1). By local, I mean environmental contexts that are experienced by a given system. In the absence of such local information, it can then be useful to take all the possible contexts. In other words, the second postulate implies that the observability of a community $\mathcal{C} \subseteq \mathcal{S}$ depends on its compatibility with environmental contexts in the actual world. Formally, according to the proposed feasibility principle, the larger the feasibility domain (preferably taking into account directions of $\boldsymbol{r}$ that can be experienced in the actual world) of a community $\mathcal{C}$, the larger the likelihood of observing such a community among all possible ones from a system $\mathcal{S}$. Previous work has shown that the size of the feasibility domain (along with constraints in the parameter space) of a community can be estimated analytically or numerically [36, 38, 54], allowing to find those communities with large values (e.g., $\max\{D(\mathcal{C}, \mathcal{S}, \mathbf{A})\}$) [39, 41, 55].

The third postulate of the feasibility principle states that community transitions (i.e., $\mathcal{C}_i \to \mathcal{C}_j$) follow the path of least feasible environmental changes (Fig. 1). These changes are evaluated under the topology of the environmental space [2, 11]. Transitions should also follow postulate (ii). In other words, the third postulate implies that observable community changes in a system are more likely the closer the feasibility domains of such communities within the environmental space and the larger the size of such feasibility domains. This postulate is reminiscent of the least action principle [56]. Formally, a transition between any two communities can happen with probability proportional to the size of their feasibility domains and inversely proportional to their distance in environmental space ($d(\mathcal{C}_i, \mathcal{C}_j)$) [57, 48, 58].

Next, I summarize current work supporting the proposed feasibility principle in community ecology. Focusing on the first postulate, theoretical work has corroborated that the feasibility domain of a community is an emergent property of its internal structure [37, 36, 54, 38]. Specifically, it has been shown that the feasibility domain is a non-reducible (or non-additive) process of the identity and number of populations in a system [45, 53]. For example, it has been shown that the addition of a population j in a system of n populations (i.e., increasing the dimensionality of the system: $\mathcal{S} \cap \{j\}$) can either leave as is or increase the feasibility domain of the n populations. Yet, the feasibility domain of the $n+1$ populations ($D(\mathcal{C}, \mathcal{S} \cap \{j\}, \mathbf{A}')$, where $\mathbf{A}'$ is the augmented interaction matrix) can have no overlap with the old feasibility domain ($D(\mathcal{C}, \mathcal{S} \cap \{j\}, \mathbf{A})$. This can also happen under the replacement of populations (e.g., changing the identity of the n population) rather than under addition or deletion [36, 45, 53]. In other words, a higher diversity (or different identity) of populations in a system can provide the opportunity to observe subsets of populations regardless of whether they cannot be previously observed under specific environmental contexts [45, 53]. Similarly, a higher diversity (or different identity) of populations in a system can remove the opportunity to observe subsets of populations regardless of whether they can be previously observed [45, 53]. Using available experimental data on the assembly of ecological communities systems under changing environments, work has confirmed that subsets of populations can be observed in late assembly stages (systems with high diversity) despite the fact that they cannot be observed in early stages (systems with low diversity)[59, 60, 39, 61]. Similarly, this work has shown that subsets of populations can be absent in late assembly stages despite the fact they can be observed in early stages [59, 60, 39, 61]. This supports the notion that each possible community $\mathcal{C} \subseteq \mathcal{S}$ is feasible for a set of environmental contexts, but such contexts change as a function of the internal structure of the system.

Shifting our focus to the second postulate of the feasibility principle, studies have found that the higher the feasibility of a community among all the possible combinations in a system, higher the chance of observing such a community in nature. Specifically, these studies have centered on the observability of plant-pollinator systems [37, 36, 46], plant-herbivore systems [55], multitrophic systems [62], and microbial systems [39, 61]. For example, studies have shown that the likelihood of observing the presence of a particular population i in a system $\mathcal{S}$ is associated with the extent to which the rest of populations $\mathcal{S} \setminus \{i\}$ increase the feasibility of population i [39, 61, 53]. Similarly, the likelihood of observing the absence of a particular population in a system is associated with the extent to which the rest of populations decrease the feasibility of such a population [39, 61, 53]. This supports the notion that feasibility is a necessary condition for the assembly of ecological communities under different environmental contexts.

Lastly, focusing on the third postulate of the feasibility principle, studies looking at community transitions have found that the smaller the feasibility changes between two communities, the higher the probability of finding transitions between them. In particular, these studies have centered on transitions in predator-prey systems [58], microbial systems [48, 57], tree systems [48], and herbivore systems [47, 48]. For example, when the system or pool of populations is fixed, work [57] has shown that the most common transitions are between communities with large feasibility domains, but the likelihood decreases the larger the changes of environmental contexts needed to make both feasible communities. In turn, when the system or pool of populations changes across time, work [47, 48] has shown that changes tend to favor systems with higher feasibility domains. This supports the notion that observable community changes $\mathcal{C}_i \rightarrow \mathcal{C}_j$ are more likely the closer the feasibility domains of such communities within the environmental space and the larger the size of such feasibility domains (conforming to the second postulate).

The story of planet Earth is a story of relentless change. However, the current rates of climate change and habitat modification are approximately 10 to 100 times greater than ever before due to anthropogenic effects [63]. This establishes the necessity to understand the challenges faced by populations when responding to their changing environments [5]. Following the feasibility principle in community ecology, studies have shown that changes in the structure of interactions associated with an increase in the feasibility domain are, in turn, associated with an increase in temperature variability [64, 65, 42]—higher latitudes with higher variations give rise to systems with higher feasibility domains. Moreover, studies have shown that populations that are able to change their interactions while increasing their feasibility domains can be more likely to be observed across a wider geographical range [46]. In this line, a series of predictions that can be made from the feasibility principle is that ecological communities will exhibit a compatibility with different environmental contexts as a function of interaction structures (following the first postulate). Higher environmental stress can lead to a reduction in the diversity of ecological communities, favoring only those with higher feasibility domains (following the second postulate). The response of ecological communities can be expected to be constrained within similar environmental contexts (following the third postulate), and therefore fragile to large environmental changes. Other challenges faced by populations during environmental change can be predicted by integrating the feasibility principle with fundamental theories in ecology [49, 16].

The sustainability of Earth's ecosystems depends on the diversity of ecological communities across space and time [31, 32, 18]. Microbial, terrestrial, and marine communities form feedback processes with the physical and chemical environment, regulating different ecosystem services and functions [66, 67]. It has been well recognized deep interconnections between climate change, biodiversity, and human health, making the understanding of the emergent behavior of ecological communities a necessary step towards successful interventions in biorestoration and biomedicine [68, 69, 70, 71, 72]. In this line, the feasibility principle in community ecology provides an opportunity to guide conservation and restoration strategies. In particular, studies have shown that the feasibility principle can explain seasonal [73, 57], historical [47], and restorative changes [74, 48] observed in different ecosystems. For example, work has shown that restoration strategies may be more likely to be successful by introducing populations one-by-one rather than all at the same time [48]. That is, the feasibility domain of a large community is expected to be both different and smaller than the union of feasibility domains generated by changing the system sequentially (following the first postulate). This sequence of introductions may be more likely to be successful by restoring subsequent communities with larger feasibility domains than the possible candidate communities (following the second postulate). If two candidate communities display a similar size of feasibility domains, restoring the community with the least changes to the predecessor's feasibility domain may lead to a higher probability of success (following the third postulate). Future work can build on the proposed feasibility principle in community ecology to increase our understanding about the self-organization and sustainability of high levels of living matter organization.

Data and code availability: No new data or code were generated. All previous data and code can be found on Github (`https://github.com/MITEcology`) and the R package feasiblityR (`https://doi.org/10.5281/zenodo.8289566`).

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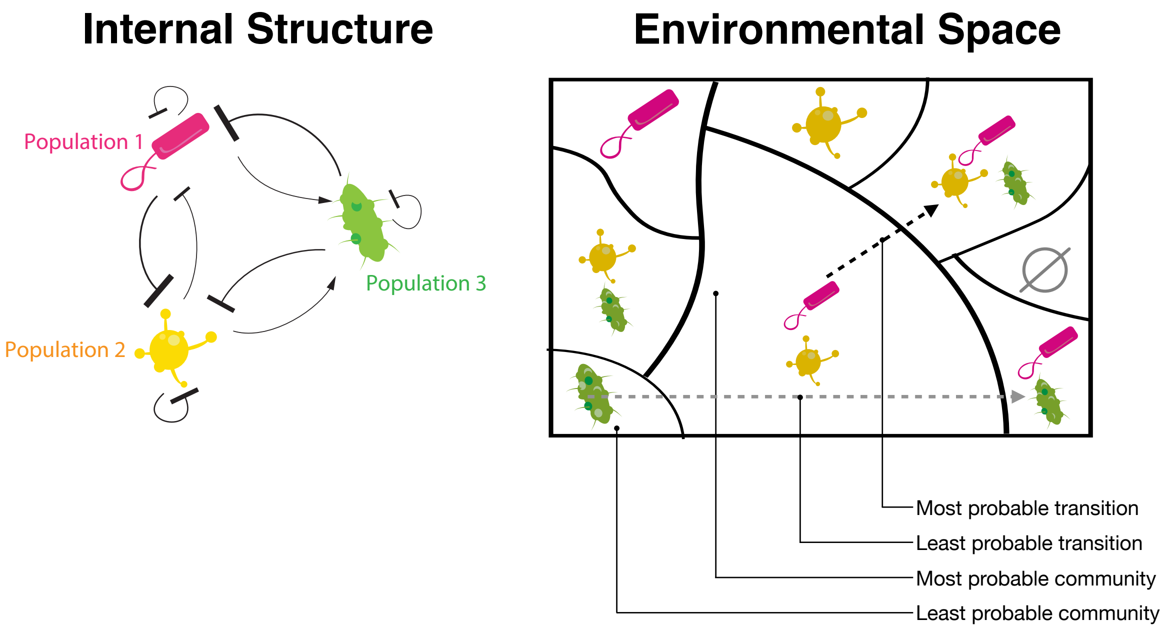

Figure 1: **Graphical representation of the feasibility principle in community ecology**. One of the ultimate goals of theoretical work is the capacity to synthesize hypotheses under a quantitative, explanatory, and predictive framework. The feasibility principle in community ecology represents an opportunity to understand the biodiversity patterns of ecological communities across environmental contexts. The proposed principle consists of three postulates: (i) Ecological communities are feasible for a set of environmental contexts constrained by their internal structure (i.e., the set of interactions determines the feasible partition in environmental space). (ii) Self-organization leads to observable communities that are feasible for the largest set of local environmental contexts (i.e., the most/least probable community to be observed has the largest/smallest feasible domain). (iii) Community transitions follow the path of least feasible changes within the environmental space (i.e., a transition between any two communities happens with probability proportional to the size of their feasibility domains and inversely proportional to their distance in environmental space).

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