Population viability in three trophic-level food chains

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Abstract

The perpetuation of three-trophic level ecosystems where the three species exhibit unpredictable time-varying survival strategies is described by a specific set, the viability kernel, gathering all states from which there exists at least one trajectory safeguarding each species over a given density threshold. The strategies permitting this property are delineated and called viable strategies. All solutions starting outside the viability kernel lead to too low densities or extinction. The viability approach highlights the timing of strategy changes necessary for a system to perpetuate itself or alternatively to lead one species to extinction.

The study of the dependence of the viability kernel on the admissible sets of strategies reveals the minimal flexibilities necessary for the existence of the system. The shape of the viability kernel determines whether the exogenous addition or substraction of prey or predator will endanger the system or not, thus gathering different experiments with opposite results. The comparison of the coexistence kernel with viability kernels for one, two or three species points out the importance of repeated strategies, not necessarily in a periodic manner, thus emphasizing the concept of repetitions in ecosystems instead of cycles as a key feature of coexistence.

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1. Introduction

Which three-trophic food chains can perpetuate themselves, and if so, how should interactions vary between the three levels, as the dynamics could sometimes lead a species to the verge of extinction? We suggest to explore this question, completing the concomitant question of persistence, which has been an important theme in population dynamics [11,12,14,13,10,9,18–20,23]. We discuss permanence, persistence and viability in Appendix A.3.

Co-evolution was presented as a dynamical game, where each individual was thought to adopt a “fitness-maximizing strategy” [6,7]. A species can then be identified to its strategy [1], or by a whole strategy set, benefiting to individuals who are not evolutionary identical [8,38,39]. Brown and Vincent [8] pointed out that the fitness of an individual in a community is bounded by evolutionary constraints. Strategies are allowed to vary only within a closed set, representing admissible bio-diversity, so that a prey species is defined by its strategy $u$, the predator by $v$, and the super-predator by $w$, within the constraints:

$$u(t) \in U, \quad v(t) \in V, \quad w(t) \in W,$$

where $U$, $V$, and $W$ are closed sets included in $[0, \infty]$. In this formulation, any predator characterized by $v \in V$ can hunt a prey of strategy $u \in U$, and any super-predator $w \in W$ can hunt a predator $v \in V$. Sih et al. [37, p. 296] for example concluded that “environmental stress can either increase or decrease the importance of predation”, and that “the outcome depends on the relative effects of stress on predation rates and on prey growth rate”. Hickman [17] showed that plants of annual species Polygonum cascadense allocate proportionally more resources to reproduction in harsh open habitats than in more moderate habitats, and that these differences are developmentally plastic, adapting to short-term environmental unpredictability. Giesel [15, p.75], from studies of passerine birds, concludes that the variability in fertility is an “important adaptation to account for environmentally induced unpredictability of the major selective forces”. Wilbur [41,43] observes the plastic growth rate and variable size at metamorphosis of amphibians as adaptations to the uncertain environment of temporary ponds, knowing that these morphological variations are induced defenses rather than a genetic polymorphism [29].

The assumption that strategies can vary within certain fixed bounds changes the kind of results to be expected: beside asymptotic patterns, all trajectories issued from all states in finite time are also worth studying. As pointed out by Law and Morton [24, p. 763] indeed, “it is not clear that local asymptotic stability is an appropriate condition for coexistence, for species may coexist
without tending to an equilibrium point” [44,16]; and the “dynamics close to an interior equilibrium point are not the main issue for coexistence”. Mittelbach et al. [30, p. 2347] acknowledged the fact that interactions within most ecological communities are often poorly known, and Wilbur [43] pointed out the inadequacies of classical models of laboratory ecologists at reflecting trajectories of communities in a changing environment.

Among the possible strategies, some are deadly: starting from a given state of food chain, does a trajectory governed by a dynamic $F$ exist which remains in a given set defining coexistence until a given time horizon? The largest set of states from which there exists at least one solution remaining in a given set $K$ forever is called the viability kernel and denoted $\text{Viab}_F(K)$ ([2,3]). Systems visiting states outside the viability kernel are doomed to go below their sufficiency thresholds. To remain in the viability kernel, the species do not really “select” strategies which are viable. The viability kernel simply reveals that, should the population densities be shifted outside of the viability kernel, then there is no way the populations could avoid rarefaction or extinction, however adaptable strategies $u$, $v$, and $w$ are, however flexible these interactions are at restructuring and hence redefining their strategies within the constraints. Mathematically, the strategies are just measurable, not necessarily continuous within their respective sets of admissible strategies $U$, $V$, or $W$. If it is impossible for infinitely flexible strategies (capable of varying instantaneously within given bounds) to rescue the situation, then adaptation under the constraints of natural selection can do no better.

This approach was used in the case of two-species Lotka–Volterra models to show that the coexistence kernel of prey and predator (from each state of this set, there exists at least one solution along which prey and predator have sufficiently high densities) is the intersection of the viability kernels of prey and of predator [4], and in [5] to build classes of ecosystem dynamics. In the two-species case, the boundaries of the viability kernels were obtained as solutions of differential equations. In extending the complexity from two to three dimensions, this method becomes hard to handle, and we resort rather to the clever viability algorithm, never used before in ecosystem dynamics, devised by Saint-Pierre [35], and presented in Appendix A. After presenting the dynamical game, we delineate the viability kernel and discuss the empirical relevance of viability in case studies. We examine the dependence of the viability kernel on the sets of admissible strategies. We then compare viability kernels for one, two or three species.

2. The dynamical game and the viability problem

We consider a food chain made of prey, predator and super-predator of respective densities $x_1(t)$, $x_2(t)$ and $x_3(t)$, in the Lotka–Volterra model of interactions:
\[
\begin{align*}
    x_1'(t) &= x_1(t)(1 - u(t)x_1(t) - v(t)x_2(t)) := f_1(x(t), u(t), v(t), w(t)), \\
    x_2'(t) &= x_2(t)(-b + \alpha v(t)x_1(t) - w(t)x_3(t)) := f_2(x(t), u(t), v(t), w(t)), \\
    x_3'(t) &= x_3(t)(-c + \beta w(t)x_2(t)) := f_3(x(t), u(t), v(t), w(t)),
\end{align*}
\]

(2)

where \(x(t) = (x_1(t), x_2(t), x_3(t))\) and where \(b > 0\) and \(c > 0\) denote rates of mortality due to factors other than predation. Setting the reproductive rate of the prey to one implies that other vital rates are implicitly scaled to this rate. \(\alpha\) and \(\beta\) are physiological parameters portraying energy transfer between trophic levels, which also govern reproductive rates of the predator and super-predator, respectively; and

\[ u(t) \in [u_{\text{min}}, u_{\text{max}}] = U, \quad v(t) \in [v_{\text{min}}, v_{\text{max}}] = V, \quad w(t) \in [w_{\text{min}}, w_{\text{max}}] = W, \]

(3)

denote the inverse of the self-limiting capacity of the prey and the predation rates respectively. \(u(t)\) describes strategies of intra-specific competition among prey, while \(v(t)\) and \(w(t)\) describe the predation strategies, in conjunction with the defense strategies of prey and predator. These strategies vary with changing heterogenous genetic structure of the population, stress, heterogeneity of the environment, and the degree of developmental flexibility of a given phenotype trait [34].

Two noteworthy examples of \(u, v, \) and \(w\) are Lotka–Volterra three-trophic level food chains obtained with \(u(t), v(t)\) and \(w(t)\) constant [46]; or Holling type 2 interactions corresponding to \(u(t) = 1, v(t) = a_1/(1 + b_1x_1(t))\) and \(w(t) = a_2/(1 + b_2x_2(t))\), where the \(a_s\) and the \(b_s\) combine intrinsic growth rates, maximum predation rates, half-saturation constants, efficiencies of predator or super-predator and the carrying capacity of the prey [22]. In these two examples, \(u, v, \) and \(w\) do not depend explicitly on time. Here, we avoid to specify \(u, v, \) and \(w\) either as constants or as functions of the states; the only thing we state on them is that they belong to closed sets.

We consider that a species is in danger when the density decreases below some fixed threshold, which, after appropriate re-scaling, we can choose as:

\[ x_1 = 1, \quad x_2 = 1, \quad x_3 = 1. \]

(4)

(The re-scaling changes the interpretation of \(1/x_1\), which represents the carrying capacity of the prey only with a factor \(1/x_1\).)

System (2) represents a dynamical game, where prey, predator, and super-predator constitute the three players, and where \(u(t), v(t)\) and \(w(t)\) represent the respective strategies at time \(t\). The dynamical game consists in having the system change so that the three species can keep the possibility at each time to survive forever: the strategies displayed by each player-species are such that they allow each player to continue playing the game, that is to say survive. In
mathematical terms, the game consists in safeguarding at least one solution of
the system remaining in a fixed closed set.

Various dynamical games can be considered, according to the point of view
of each protagonist:

• **Viability of the prey:**
The subset of $K_1: = [1, \infty[ \times [0, \infty[ \times [0, \infty[$ is viable if and only if, for any initial condition $(x_1(0), x_2(0), x_3(0))$ of prey, predator and super-predator densities, there exists at least one solution $(x_1(\cdot), x_2(\cdot), x_3(\cdot))$ of Eq. (2) regulated by strategies $u(\cdot), v(\cdot), w(\cdot)$ satisfying (3) which complies to the constraints:

$$
\text{for all } t \geq 0, \ x_1(t) \geq x_1 = 1, \ x_2(t) \geq 0, \ x_3(t) \geq 0.
$$

(5)

• **Viability of the predator:**
Similarly, if attention is paid to the predator, only the populations of predator maintaining themselves above the threshold $y$ are viable. The set of constraints is thus $K_2: = [0, \infty[ \times [1, \infty[ \times [0, \infty[$;

• **Viability of the super-predator:**
The set within which to remain is $K_3: = [0, \infty[ \times [0, \infty[ \times [1, \infty[$;

• **coexistence of super-predator, predator and prey:**
A point $x^0 = (x_1^0, x_2^0, x_3^0)$ belongs to the food chain coexistence kernel if there exists at least one solution $x(\cdot) = (x_1(\cdot), x_2(\cdot), x_3(\cdot))$ of the dynamical game made of Eqs. (2) and (3) starting from $x^0$ and satisfying:

$$
\text{for all } t \geq 0, \ x_1(t) \geq x_1 = 1, \ x_2(t) \geq x_2 = 1, \ x_3(t) \geq x_3 = 1,
$$

that is to say, remaining in a given set $K$:

$$
x(t) \in K := K_1 \cap K_2 \cap K_3.
$$

(7)

We study here the coexistence kernel for the three trophic levels. Eqs. (2) and (3) can synthetically be written into the differential inclusion:

$$
x'(t) \in F(x(t)),
$$

(8)

under constraints

$$
x(t) \in K,
$$

(9)

where:

$$
F(x(t)) := \{ (x_1(t)(1 - u(t)x_1(t) - v(t)x_2(t)), x_2(t)(-b + ax(t)x_1(t) - w(t)\beta(t)x_3(t)), x_3(t)(-c + \beta w(t)x_2(t))) | u(t) \in U, v(t) \in V, w(t) \in W \}
$$

$$
:= \{ f(x, u, v, w) | u(t) \in U, v(t) \in V, w(t) \in W \}
$$

(10)

is a point-to-set map, also called correspondence.

Aubin [2] showed the existence of the viability kernel of the set $K$, the largest closed viable set in $K$ under the dynamic $F$. 
3. Results

3.1. The viability kernel

Now, not only the equilibrium set and attractors characterize an ecosystem, but also the viability kernel. This is our main result: define the viability kernel and delineate it in the case of three-trophic food chains. It is represented in Fig. 1 for certain values of $U$, $V$ and $W$. In this example, not all states in $K$ are viable: from these nonviable states, the system is doomed to leave $K$ sooner or later. The viability kernel is then smaller than the set of state constraints. Many states which lie outside attractors (notably equilibria) are nonetheless viable: starting from these states, the food chain can perpetuate itself forever.

The maintenance forever depends on the selection at each time of viable interactions $u$, $v$, and $w$: these viable interactions are defined as those for which there exists at least one route remaining in $K$ forever, then which makes the direction $x'(t)$ at $t$ belong to a specific set, the contingent cone, which extends the concept of tangent space to any closed set.

For any set $M \subset X$, the contingent cone $T_M(x)$ at state $x$ is defined by

$$T_M(x) = \left\{ \tilde{x} \in IR^3; \liminf_{h \to 0^+} \frac{1}{h} d_M(x + h(\tilde{x})) = 0 \right\},$$

Fig. 1. Viability kernel of the three-trophic food chain: $U = [0.20;0.21]$, $V = [0.12;0.13]$, $W = [0.10;0.11]$: from each state of this set, there exists at least one trajectory remaining in the set of state constraints forever.
where \( d_M(x) = \inf_{w \in M} \|w\| \). If \( M \) is convex, \( T_M \) coincides with the tangent cone used in convex analysis.

Aubin [2] showed that if the set \( \tilde{K} \) is a viability domain, then it satisfies the tangential condition:

for all \( x \in \tilde{K} \) there exists \( u \in U, v \in V, w \in W \) such that

\[
(f_1(x, u, v, w), f_2(x, u, v, w), f_3(x, u, v, w)) \in T_{\tilde{K}}(x).
\]

(11)

In the interior of the viability kernel, all strategies \( u, v, \) and \( w \) are viable. The difficulty lies on the boundary of the viability kernel. As an example, Fig. 2 shows a viable strategy \( v(t) \) on the boundary in the direction of high super-predator density of the viability kernel of Fig. 1. This strategy appears very irregular, alternating abruptly between \( v_{\text{min}} \) and \( v_{\text{max}} \). Remaining along this boundary thus demands strategies flexible in time: the system is easy to destabilize when the super-predator is important in density. Viable strategies on the lower boundary are smoother though not constant, implying that coexistence is obtained with less variation of the interactions when the super-predator is of low density. We do not say that these strategies correspond to actual species,
we just say that on the boundary, which is an extreme case, these strategies would enable a system to remain in $K$, but actual species do not have to follow the boundary, they can travel more smoothly in the interior of $K$.

3.2. Empirical relevance

Empirical studies where viable and nonviable strategies are estimated are few, because nonviable species in nature are doomed to extinction, and because of the evolutionary scale of time, which renders experiments often impractical [37]. However, Luckinbill [26] studied predator *Didinium nasutum* and prey *Paramecium aurelia*, itself feeding on *Aerobacter aerogenes*. Attempts at the prolonged laboratory study in these cultures “lacking refuges or physical complexity” lead to the extinction of the predator. The coexistence is obtained only when he added methyl cellulose into the culture, which has the “important effect of reducing the rate of movement of both *P. aurelia* and *D. nasutum* without giving the prey a dispersal advantage” (p. 1322). The ensuing reduced frequency of encounter between predator and prey enhances the ability of both species to coexist, provided that the availability of nutrient is fine-tuned. It is indeed necessary in this experiment “both that predators be unable to capture all the prey in the system and that some restriction of prey growth exist in addition to predation” (p. 1326). If we view this experiment within the framework of Eq. (2), we understand interactions $u$, $v$, and $w$ in the absence of methyl cellulose as nonviable. Slowing down the movements renders them viable, and nutrient is adjusted so that the initial state becomes viable.

Another related case study is offered by Wilbur [41,42]. He showed that only small tadpoles are killed by predaceous insects, and that rapid growth appears as a defense against such gape-limited predators. Slow growth leads to the complete elimination of tadpoles, unless tadpoles are sufficiently dense to satiate predators. Rapid growth and morphological metamorphoses constitute then viable strategies; a long larval period and the morphology prevailing in the absence of predators become nonviable in presence of predators. Moreover, he demonstrates the role of initial conditions and history in determining the trajectory of a community, thus in coherence with the logic of the viability kernel, which is a set of initial conditions. This example of tadpoles is a fascinating case study where the group is on the verge of being totally devoured: then, for certain initial conditions in tadpoles and newts, metamorphoses of tadpoles confronted with predations permit a few individuals to escape. We are in the logic of viable strategies, viable initial states, and viability boundary.

Wilbur [40, p. 2293] varied again initial conditions in an array of 144 experimental ponds in which he could follow the course of the community structure throughout a season. Tadpoles with thin tails survive if their density is high enough so as to satiate newts: the system remains in the interior of the coexistence kernel and there is no need to change interactions. But newly migrated
predators “can reduce, even eliminate, prey, and these risks change with relative body sizes of predator and prey” (p. 2280). When tadpole density collapses, individuals decrease active foraging or develop morphological adaptations, such as changes in coloration and widening of tails, accelerate growth by shortening of the larval period. These phenotypic changes permit the survival of the biggest tadpoles, which are few then. Tadpoles with wider tails swim faster to escape predator *Anax*, but in the absence of predator, have a higher mortality than tadpoles with narrower tails. Coloration or the width of the tail constitute viable strategies, while narrow tails and normal color become nonviable in the presence of predators. The viability view is thus in total accordance with classical Darwinism (in the absence of predators, tadpoles with narrower tails have a selective advantage), it just points out the necessity of strategy changes when a certain limit is attained, and this limit is the viability boundary. The viability argument emphasizes the timing of metamorphoses: when should they occur for some tadpoles to escape? The answer is: necessarily, the last moment is when the viability boundary is attained.

Although these experiments were not specifically designed to reveal viability kernels, they offer a striking example of a prey changing sufficiently rapidly its interactions with its predators so as to render their population viable. *The concept of viable strategies having to change suddenly when the viability kernel is attained is coherent with the observed sudden change of strategies enabling a few tadpoles to survive.* We are not saying that viability arguments are sole to explain these experiments, and we are not antagonistic with more familiar explanations in terms of ESS. We are just presenting a theoretical framework, compatible with these experiments, valid in transient time, and based on the mere survival or not of species.

### 3.3. Coexistence depends on the range of admissible strategies

The viability kernel increases with the sets *U*, *V*, and *W* of admissible interactions, as Table 1 shows.

|                         | Coefficient | std  |
|-------------------------|-------------|------|
| Intercept               | 12.44       | 0.67 |
| $u_{\text{min}}$        | −12.03      | 1.41 |
| $u_{\text{max}}$        | 19.40       | 1.29 |
| $v_{\text{min}}$        | −40.48      | 1.53 |
| $v_{\text{max}}$        | 9.80        | 1.51 |
| $w_{\text{min}}$        | −51.73      | 1.16 |
| $w_{\text{max}}$        | 16.97       | 1.16 |
Its volume is empty when $U$, $V$ or $W$ are narrow enough (species behaviour is too rigid to face environment change), then increases rapidly in a logistic manner to reach an upper limit, equal to the set $K$ itself. Fig. 3 shows how the volume of the viability kernel increases with the most influencing bounds, $v_{\text{min}}$ for the predator, and $w_{\text{min}}$ for the super-predator. This Fig. 3 emphasizes that the coexistence of the three species needs that the super-predator must repeatedly take a sufficiently low capture rate $w$, and that the predator cannot have too high its own strategy $v$. This stands in accordance with more classical theory on asymptotic time horizons that predator prey systems are endangered when predators are too effective, devoring prey far below the capacity of the prey to restock the milieu. The repetition of sufficiently low values for $v$ does not have to be cyclic, it depends on where the system travels within the viability kernel (if it remains viable). The search for cyclic patterns in empirical systems could then be completed by the search of mere repetitions.

Equilibria within the set of constraints by definition belong to the viability kernel. The viability kernel also contains all transient states from which
coexistence is possible forever: adding nutrients sufficiently shifts the initial state out of the viability kernel, where the interactions $u(t)$, $v(t)$ and $w(t)$ are no longer flexible enough to restore the possibility to remain in the set of constraints forever. The viability kernel thus permits to address the rarefaction or the extinction of prey or predators resulting from oscillations of high amplitude, as they tend to be in enriched systems, in the larger case of time varying strategies and in transient time (not at attractors). Moreover, it permits to identify viable strategies when the system is prone to high amplitude oscillations. If the disturbance is not of high enough amplitude, leaving the system within the viability kernel, the species continue to coexist (such as in [28], studying Daphnia feeding on algae). A sufficient exogenous addition of predator (or of super-predator) can push the state out of the viability kernel, implying by definition the destruction of the system before long.

Predators Didinium and Woodruffia added in sufficient quantity can lead either to extinction [31], or to coexistence for long periods [26,27,36]. This different response depending on the quantities of predators added and on other conditions enters into the very principle of viability. Fig. 4 shows a trajectory starting from a viable state $B$: it remains within $K$ and converges in this case to

![Fig. 4. Example of a trajectory starting from viable state $B$. After a shift in prey density, no trajectory can ever maintain the prey over the threshold density. Such a trajectory starts from the nonviable state $A$.](image)
an equilibrium. Shifting the density of prey so that the new initial state \( A \) is outside the viability kernel, there is no trajectory any longer remaining within \( K \) (defined in Eq. (7)). Fig. 4 shows an arbitrary solution starting from \( A \): while rolling around, it leaves \( K \), driving the prey to attain too small densities.

The same holds true for the predator: shifting the predator density \( x_2 \) to too high a value, so that the starting state is outside of the viability kernel, leads the system to violate the constraints. Symmetrically, starting from too low a density in predator has the same effect, because of the shape of the viability kernel represented on Fig. 1, leaving states with low values of prey and predator non-viable. In this case, adding predator drives the system to a new initial state which is viable. Concerning the predator, this property of the viability kernel complies with Mittelbach et al. [30] who showed that the elimination and reintroduction of a top predator in Wintergreen Lake dramatically changed the species composition and size structure of the fish and zooplankton communities.

The shape of the viability kernel on Fig. 1 also implies that this property of changing the viability of the new initial state does not hold for the super-predator: adding super-predator does not threaten the conservation of the three species as long as the initial state after the addition of super-predator still lies within the viability kernel. This complies with Morin and Lawler [31] who found no consistent effects of omnivores on prey dynamics for two omnivore species feeding on two different prey. For too high an addition, the initial state is shifted outside of the viability kernel and the system is then doomed to cross the constraints. Varying the capture rate \( w \) of the super-predator alters the kernel, but does not change the projection onto the prey-predator plane significantly: no nonviable state can be rendered viable by the addition of super-predator. Muratori and Rinaldi [32] showed theoretically that Holling type interactions permit that the addition of a suitable super-predator with linear functional response to a standard prey-predator system characterized by stable limit cycle can give rise to a food chain with a unique positive stable equilibrium. However, this theoretical stabilizing effect does not account for the violation or not of the constraints during the process. The consideration of constraints also during the transient trajectories is a plus brought by viability theory.

3.4. Comparison of viability kernels for one, two or three species

So far, we paid attention only to the coexistence kernel \( \text{Viab}_F(K_1 \cap K_2 \cap K_3) \). The comparison of this coexistence kernel with viability kernels for a single species yields the initial states from which there exists at least one solution maintaining this species while rarefying the two others. The set \( \text{Viab}_F(K_i) \), represented in Fig. 5, is the set of all initial states from which there exists at least one solution for which the prey is always above its threshold \( x_1 \), no matter what
happens to the prey and to the predator: they can cross their own density thresholds $x_2$ and $x_3$, and even go extinct. All solutions starting from states belonging to $\text{Viab}_F(K_1)$ but not to the coexistence kernel (for example for low values of prey and predator, just above their thresholds) cross the thresholds $x_2$ of predator or $x_3$ of super-predator at least once: from these states, it is then possible to rarefy predator and super-predator while preserving the prey.

The viability kernel $\text{Viab}_F(K_2)$ of $K_2$ is the set of all initial states for which the density of the predator remains greater or equal than the threshold $x_2$, even at the price of a rarefaction of the prey under $x_1$, or of the super-predator $x_3$. As expected, states for which all solutions encounter $x_1 = 0$ remain there and are nonviable. From states belonging to $\text{Viab}_F(K_2)$ but not to $\text{Viab}_F(K_1)$ (for example states for which $x_1$ is just under its threshold $x_1$), there exists at least one solution maintaining the predator over its threshold, but no solution preserving the prey over $x_1$. From states belonging to $\text{Viab}_F(K_3)$ but neither to $\text{Viab}_F(K_1)$ nor to $\text{Viab}_F(K_2)$, there exists a possibility to maintain the density of super-predator over $x_3$ but at the sure price of reducing prey and predator under their respective thresholds for a while (not necessarily simultaneously). Similarly, the comparison with viability kernels for two species gives the initial states from which there exists at least one possibility to maintain them both while the other species will rarefy at least for a while.

The various viability kernels in Fig. 5 thus delineate a typology of initial states from which one species is doomed to go below its threshold and another has at least one chance to be maintained over its own threshold forever. Such a
typology is in the logic of the experiments of Wilbur [40] who manipulated initial conditions in densities of tadpoles and newts.

The inclusion of the coexistence kernel in Viabₚ(Kᵢ ∩ Kⱼ) and in Viabₚ(Kᵢ), i, j = 1, 2, 3 comes from the definition of the viability kernels. Although Viabₚ(K₁ ∩ K₃) and Viabₚ(K₃) do not appear different on the perspective of Fig. 5, the former is strictly included in the latter, as Viabₚ(K₃) includes states in x₁ < x₃, where the super-predator can survive for a while over its threshold even with rarefied prey. The same holds true with Viabₚ(K₁ ∩ K₂) strictly included in Viabₚ(K₂), and the coexistence kernel strictly included in Viabₚ(K₂ ∩ K₃).

Moreover, the viability kernel of an intersection has no reason to be the intersection of the viability kernels: for example, in Fig. 5, Viabₚ(K₂ ∩ K₃) ≠ Viabₚ(K₂) ∩ Viabₚ(K₃): from all states of this latter set, there exists at least one trajectory maintaining x₂ ≥ x₂ and at least one trajectory maintaining x₃ ≥ x₃, but there is no reason why there should exist one trajectory maintaining both (which is the case in Viabₚ(K₂ ∩ K₃)). Biologically speaking, coexistence is not solved by the separate consideration of each species.

4. Conclusion

Lawton [25] pointed out that predictions of food web theory are relatively bad on natural populations. We precisely acknowledged the unpredictability of environment and the diversity of species interactions through u, v, and w varying within closed sets, and suggested instead that the concept of viability adds to our understanding of transient population dynamics, beside more familiar ESS theory, in addressing the question of the maintenance of a system within density thresholds.

- We then identified the three-trophic food chain to a dynamical game, where interactions are viewed as strategies varying in closed sets. This led us to define and build the viability kernel, which should take its place beside the concepts of equilibria and attractors.
- We discussed the empirical relevance of viability arguments, in Luckinbill [26] and in Wilbur [40–42]. Notably, the observed sudden change of strategies of tadpoles when the population is on the verge of being totally devoured by newts in Wilbur’s study is coherent with the viability kernel, where all strategies are viable in the interior of the viability kernel, but only a few ones on the viability boundary.
- The dependence of viability kernels on sets of strategies showed both the minimum range of variations in strategies for coexistence, the importance of minimal predation rates, or the minimal flexibility required for the three-trophic food chain to work.
• The very shape of the viability kernel is coherent with case studies where the exogenous addition of one species leads either to extinction of one species or on the contrary does not threaten coexistence, depending on where the state of the system was in the viability kernel at the moment of the addition.

• The comparison of viability kernels for one, two or three species showed the importance of repetitions in time of certain strategies, which are not necessarily cyclic.

Morin and Lawler [31] called for a better understanding of the organizing forces in ecosystems: the bare mathematical translation of having the three species remaining within closed sets adds an organizing principle stemming from the confrontation of intrinsic dynamics and constraints, in addition to classical selective arguments. Nagumo [33] pioneered the mathematics of remaining within a closed set $K$ in the case of a differential equation. The addition of set-valued analysis pioneered by Aubin [2] allows us to take into account the variability and unpredictability inherent in ecosystem dynamics, and the concept of viability kernel permits to delineate specific states, the viable states, answering the question of the perpetuation of the ecosystem not only asymptotically, but also in transient time.

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Appendix A. The viability algorithm [35]

A.1. Characterization of the dynamics $F$

The question: ‘when can we say that $\forall t \geq 0 x(t) \in K$?’ can be correctly addressed when $F$ is convex, upper semi-continuous with compact images and $K$ compact.

• The image $F(x)$ is bounded, and, as the dimension of the state space is finite, it is also compact.

• The convexity of $F(x)$ results from its linearity in $u$, $v$, and $w$.

• How regular is the process? Do small variations on $x(t)$ result in large variations on $x(t + dt)$? This property is not necessary to apply viability theorems, but it is useful to run the numerical viability algorithm. For any fixed $u$, $v$, $w$, does it exist $l \in [0, 1]$ such that:

$$\forall x, y \in K, \sup_{(u,v,w) \in U \times V \times W} | f(x, u, v, w) - f(y, u, v, w) | \leq l |x - y|, \quad (12)$$
which implies the Lipschitz property:

\[ F(x) \subseteq F(y) + l\|x - y\|. \]  (13)

Such a value exists because \( f \) is differentiable with respect to \( x \in X \) at fixed \( u, v, w \), and the components of \( \frac{\partial f_i}{\partial x_i} \) for \( i = 1, 2, 3 \) respectively are bounded on \( K \). The Lipschitz property of \( F \) on \( K \) implies that \( F \) is continuous (a fortiori upper semi-continuous).

\( F \) has thus the required property of being Lipschitz, and \( K \) is obviously compact. We can thus define the numerical approximation of the discrete-time viability kernel.

A.2. Numerical approximation of the discrete-time C-viability kernel

The difficulty is to represent \( F(x) \) on a convenient grid of the state space. This question was addressed by Saint-Pierre [35], whose algorithm makes it possible to compute viability kernels.

When the correspondence is Lipschitz on \( K \), Saint-Pierre considered the approximation \( F_e \) of the correspondence \( F \):

\[ F_e(x) := F(x) + \epsilon M(x) \ell(x) \mathcal{B}, \]  (14)

where \( \mathcal{B} \) is the unit ball, \( M(x) = \sup_{y \in F(z), z \in x + B} \|y\| \) is an estimation of a local bound of the correspondence, \( \ell(x) \) is the Lipschitz constant of \( F \) in a neighborhood of \( x \), and \( \mathcal{B} \) is the unit ball of \( X \).

Consider a grid \( X_h \) of \( X \) associated with any \( h > 0 \) such that:

(i) the set \( X_h \) has a finite intersection with any compact of \( X \);
(ii) \( \forall h > 0, \forall x \in X, \exists x_h \in X_h, \|x - x_h\| < h \)

and the projection of the correspondence \( F_e(x) \) onto \( X_h \), defined by

\[ F_{\epsilon,h}(x_h) = F_e(x_h) \cap X_h. \]  (15)

Then, for a sequence \( (x_h^{(n)})_{n \in \mathbb{N}} \) on \( X_h \), the initial dynamic (8) becomes the approximated discrete system [35]:

\[ x_h^{(n+1)} \in F_{\epsilon,h}(x_h^{(n)}). \]  (16)

For

\[ K_h = (K + h \mathcal{B}) \cap X_h, \]  (17)
the discrete viability kernel \( \text{Viab}_{F,e,h}(K_h) \) is the set of initial values \( x^0_h \in K_h \) of a solution \( (x^{(n)}_h)_{n \in \mathbb{N}} \) of (16) satisfying \( x^{(n)}_h \in K_h \) for all \( n \in \mathbb{N} \). To calculate \( \text{Viab}_{F,e,h}(K_h) \), the sequence of sets \( K^{(n)}_{e,h} \) is built according to the algorithm:

\[
\begin{align*}
K^0_{e,h} & := K_h, \\
K^{(n+1)}_{e,h} & := \{ x_h \in K^{(n)}_{e,h} \text{ such that } F_{e,h}(x_h) \cap K^{(n)}_{e,h} \neq \emptyset \}.
\end{align*}
\]

Saint-Pierre [35] showed that if \( F \) is a Lipschitz correspondence, with compact images, then:

\[
\lim_{n \to \infty} K^{(n)}_{e,h} = \text{Viab}_{F,e,h}(K_h)
\]

and

\[
\lim_{\varepsilon \to 0+} \lim_{\varepsilon \to 0+} \text{Viab}_{F,e,h}(K_h) = \text{Viab}_F(K).
\]

A.3. Persistence, permanence, and viability

Aubin [2, p. 128; 45, p. 240] showed how permanence is a specific case involving viability: consider a closed set \( K \) containing a set \( \Omega \) in the phase space, such that

\[
\Omega \subset \text{Int}(K) \quad \text{and} \quad \partial K = \text{Viab}_F(K \setminus \Omega),
\]

where \( \text{Viab}_F(M) \) denotes the viability kernel of the set \( M \) under dynamics \( F \), which is the largest set of initial conditions from which there exists at least one solution of \( x' \in F(x) \) remaining in \( M \) forever. The first condition opens the opportunity of the existence of asymptotic states without extinction of any species. The second condition reflects the fact that the system can no longer escape the boundary \( x_i = 0, \ i = 1, 2 \) or 3 once it is attained: there is no way to recover an extinct species. Permanence occurs in the special case when \( \Omega \) is invariant, that is to say all solutions starting from \( \Omega \) remain in \( \Omega \). What is important is that the boundary is not hit from a solution starting from \( \Omega \), a property which was simplified, in the statement of permanence, into the existence of a \( \delta > 0 \) such that \( \delta < \liminf_{t \to \infty} x_i(t) \): the system eventually confines away from extinction with a “security” ring of width \( \delta \). The system can remain under the threshold \( \delta \) for a long time before the interesting property appears.

1 The arrow over \( \text{Viab}_{F,e,h}(K_h) \) emphasizes the discrete nature of the construction. This set is the set of points from which there exists a solution \( (x^{(n)}_h)_{n \in \mathbb{N}} \) remaining in \( K_h \).
This is not true with viability where the question is to satisfy or not the constraints at each time.

Permanence is a more stringent property than strong persistence, which requires \( \delta = 0 \), and persistence which requires \( 0 < \limsup_{t \to \infty} x_i(t) \) [18, p. 161]. Indeed, as \( \liminf \leq \limsup \), permanence implies persistence. However, the concept of \( \limsup \) is hard to generalize outside the simplex. Having persistence without strong persistence is a very particular concept, meaning that an almost extinct \( x_i \) will reappear in the future, and was forged notably for the Lotka–Volterra model [21]. Local stability says that there exists a neighborhood \( V_1 \), such that for any neighborhood \( V_2 \subset V_1 \), there exists a neighborhood \( V_3 \) such that any solution starting from \( V_3 \) returns to \( V_2 \). This asymptotic property is also specific of the simplex and hard to generalize in general sets.

References

[1] P.A. Abrams, Alternate models of character displacement. I. Displacement when there is competition for nutritionally essential resources, Evolution 41 (1987) 651–661.
[2] J.-P. Aubin, Viability Theory, Birkhäuser, Boston, 1991.
[3] J.-P. Aubin, A. Bayen, N. Bonneuil, P. Saint-Pierre, Viability, Games, Control, Springer-Verlag, in press.
[4] N. Bonneuil, K. Müllers, Viable populations in prey-predator systems, J. Math. Biol. 35 (1997) 261–293.
[5] N. Bonneuil, Making ecosystem models viable, Bull. Math. Biol. 65 (2003) 1081–1094.
[6] J.S. Brown, T.L. Vincent, The evolutionary game, Theor. Popul. Biol. 31 (1985) 140–166.
[7] J.S. Brown, T.L. Vincent, Coevolution as an evolutionary game, Evolution 41 (1) (1987) 66–79.
[8] J.S. Brown, T.L. Vincent, Organization as an evolutionary game, Evolution 46 (5) (1992) 1269–1283.
[9] H. El-Owaidy, A.A. Ammar, Mathematical analysis of a food-web model, Math. Biosci. 81 (1986) 231–237.
[10] H.I. Freedman, J.W.H. So, Global stability and persistence of simple food chains, Math. Biosci. 76 (1985) 69–86.
[11] H. Freedman, P. Waltman, Mathematical analysis of some three species food-chain models, Math. Biosci. 33 (1977) 257–276.
[12] H.I. Freedman, P. Waltman, Persistence in models of three interacting predator-prey populations, Math. Biosci. 68 (1984) 213–231.
[13] T.C. Gard, Persistence in food webs, Holling-type food chains, Math. Biosci. 49 (1980) 61–67.
[14] T.C. Gard, T.G. Hallam, Persistence in food-webs-I, Lotka–Volterra food chains, Bull. Math. Biol. 41 (1979) 877–891.
[15] J.T. Giesel, Reproductive strategies as adaptations to life in temporally heterogeneous environments, Ann. Rev. Ecol. Syst. 7 (1976) 57–79.
[16] A. Hastings, Food web theory and stability, Ecology 69 (1988) 1665–1668.
[17] J.C. Hickman, Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae), J. Ecol. 63 (1975) 681–701.
[18] J. Hofbauer, K. Sigmund, The Theory of Evolution and Dynamical Systems, Cambridge University Press, Cambridge, 1988.
[19] J. Hofbauer, K. Sigmund, Evolutionary Games and Population Dynamics, Cambridge
University Press, Cambridge, 1998.
[20] V. Husson, R. Law, Permanence and the dynamics of biological systems, Math. Biosci. 111
(1992) 1–71.
[21] V.A.A. Jansen, K. Sigmund, Shaken not stirred, on permanence in ecological communities,
Theor. Popul. Biol. 54 (1998) 195–201.
[22] Y.A. Kuznetsov, S. Rinaldi, Remarks on food chain dynamics, Math. Biosci. 134 (1996)
1–34.
[23] R. Law, J.C. Blackford, Self-assembling food webs, a global viewpoint of coexistence of
species in Lotka–Volterra communities, Ecology 73-2 (1992) 567–578.
[24] R. Law, D. Morton, Permanence and the assembly of ecological communities, Ecology 77 (3)
(1996) 762–775.
[25] J.H. Lawton, Food webs, in: J.M. Cherrett (Ed.), Ecological Concepts, Blackwell Scientific,
Oxford, 1989, pp. 43–78.
[26] L.S. Luckinbill, Coexistence in laboratory populations of Paramecium aurelia and its predator
Didinium nasutum, Ecology 54 (1973) 1320–1327.
[27] L.S. Luckinbill, The effects of space and enrichment on a predator-prey system, Ecology 60
(1974) 1098–1102.
[28] E. McCauley, W.W. Murdoch, Predator-prey dynamics in environments rich and poor in
nutrients, Nature 343 (1990) 455–457.
[29] S.A. McCollum, Ecological consequences of predation-induced polyphenism in larval hylid
frogs, Dissertation. Duke University, Durham, North Carolina, USA, 1993.
[30] G. Mittelbach, A. Turner, D. Hall, J. Rettig, C. Osenberg, Perturbation and resilience, a long-
term, whole-lake study of predator extinction and reintroduction, Ecology 76 (8) (1995) 2347–
2360.
[31] P.J. Morin, S.P. Lawler, Food web architecture and population dynamics. Theory and
empirical evidence, Ann. Rev. Ecol. Syst. 26 (1995) 505–529.
[32] S. Muratori, S. Rinaldi, Low- and high-frequency oscillations in three-dimensional food chain
systems, SIAM J. Appl. Math. 52 (6) (1992) 1688–1706.
[33] M. Nagumo, Über die Lage der integalkurven gewöhnlicher Differentialgleichungen, Proc.
Phys. Math. Soc. Jpn. 24 (1942) 551–559.
[34] E.R. Pianka, Evolutionary Ecology, Harper and Row Publishers, New York, 1978.
[35] P. Saint-Pierre, Approximation of the viability kernel, Appl. Math. Optimis. 29 (1994) 187–
209.
[36] G.W. Salt, Predation in an experimental protozoan population Woodruffia-Paramecium, Ecol.
Monogr. 37 (1967) 113–144.
[37] A. Sih, P. Crowley, M. McPeek, J. Petranka, K. Strohmeier, Predation, competition, and prey
communities, a review of field experiments, Ann. Rev. Ecol. Syst. 16 (1985) 269–311.
[38] T.L. Vincent, J.S. Brown, Evolution under nonequilibrium dynamics, in Mathematical
Modelling in Science and Technology, Proceedings of the Fifth ICMM 29–31 (8) (1986) 766–
771.
[39] T.L. Vincent, J.S. Brown, The evolutionary response of systems to a changing environment,
Appl. Math. Comput. 32 (2–3) (1989) 185–206.
[40] H.M. Wilbur, Experimental ecology of food webs, complex systems in temporary ponds,
Ecology 78 (8) (1997) 2279–2302.
[41] H.M. Wilbur, Regulation of structure in complex systems, experimental temporary pond
communities, Ecology 68 (1987) 1437–1452.
[42] H.M. Wilbur, Salamander predation and the structure of experimental communities, anuran
responses, Ecology 64 (6) (1983) 1423–1429.
[43] H.M. Wilbur, Competition, predation, and the structure of the Ambystoma-Rana sylvatica
community, Ecology 53 (1972) 3–21.
[44] M. Williamson, Are communities ever stable? in: A.J. Gray, M.J. Crawley, P.J. Edwards (Eds.), Colonization, Succession and Stability, Blackwell Scientific, Oxford, 1987, pp. 353–371.
[45] J.-P. Aubin, Dynamic Economic Theory, Springer, Berlin, 1997.
[46] A. Rescigno, K.G. Jones, The struggle for life, III. A predator–prey chain, Bull. Math. Bioph. 34 (1972) 521–532.