Disruption of biological processes in the Anthropocene: the case of phenological mismatch

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Disruption of biological processes in the Anthropocene: the case of phenological mismatch

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Abstract

Biologists increasingly report anthropogenic disruptions of both organisms and ecosystems, suggesting that these processes are a fundamental, qualitative component of the Anthropocene. Nonetheless, the notion of disruption has not yet been theorized in biology. To progress in that regard, we work on a special case. Relatively minor temperature changes impact plant-pollinator synchrony, disrupting mutualistic interaction networks. Understanding this phenomenon requires a specific rationale since models describing them use both historical and systemic reasoning. Specifically, history justifies that the system is initially in a very narrow part of the possibility space where it is viable, and the disruption randomizes this configuration. Building on this rationale, we develop a formal framework inspired by Boltzmann's entropy. With empirical networks, we show historical trends depending on latitude. Then we propose an initial definition of disruption in ecology. When a specific historical outcome contributes to a system's viability, disruption randomizes this outcome, decreasing viability.

Keywords: disruption, historicity, plant-pollinator networks, entropy, philosophy of science, closure of constraints

Contents

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1 Introduction

A strategy to analyze human activities' impact is to exhibit the sustained decline of several quantities, such as freshwater supplies per individual or forest area. This rationale is at the core of the "warning to humanity" cosigned by more than sixteen thousand scientists (Ripple et al., 2017). However, this rationale, inherited from physics, is insufficient to understand many anthropogenic effects, and we feel the need for synthetic concepts to address the anthropogenic disorganizations of the living.

Scientists frequently use the notion of *disruption* to account for the direct and indirect detrimental consequences of human activities on the living. Many articles describe, for example, disruptions of trophic networks (food webs), disruptions caused by climate change, and endocrine disruptors. However, this notion has not yet been the subject of a systematic conceptualization or theoretical investigation.

By contrast, the concept of disruption as a strategy of economic innovation has been theorized in the '90s. In this sense, disruptions are new strategies that transform a market or activity structure, typically with digital technologies (Dru, 1996; Christensen et al., 2015). In addition, recent philosophical work describes the disruption of human societies, arguing that today's technological innovations are faster than society's ability to incorporate them by sciences, politics, customs, and laws. Then societies cannot

domesticate their technological productions, leading to widespread toxic consequences for both human and non-human living beings (Stiegler, 2019).

The use of the term disruption in biology is, however, older than in economics. For example, scientists describe the disruptions of mutualisms at least since the 80's (Bond & Slingsby, 1984). The increasing use of the word "disruption" seems associated with environmental issues, as shown by the example of endocrine disruptors (chemicals disrupting hormone actions, Colborn & Clement, 1991; Gore et al., 2015). Moreover, its use grows steadily in ecology (fig. 1).
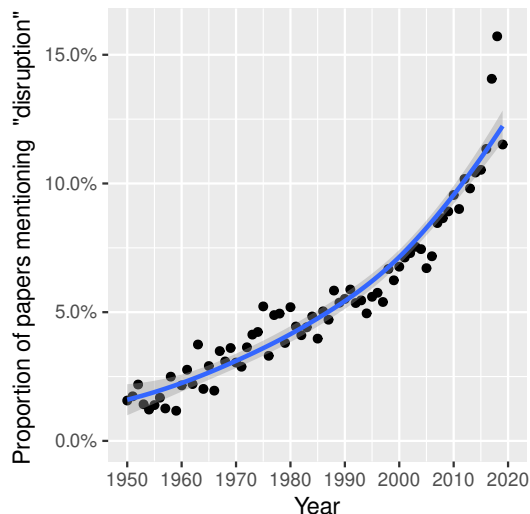

Figure 1: *Occurrences of the term "disruption" and derivatives in ecology publications from 1950 to 2019.* The curve represents the ratio of papers mentioning *disruption* or derivatives (*disrupt*, *disrupts* and *disrupted*) and *ecology* over papers mentioning *ecology* in the JSTOR database, in the fields of Ecology & Evolutionary Biology and Environmental Science.

In this context, it is critical to conceptualize and theorize the notion of disruption in biology. Biological disruptions should be distinct from existing concepts and have theoretical specificity. It should be distinct from the familiar concept of perturbation existing in physics and its root in specific mathematical methods — chiefly small perturbations around equilibrium.

In English, to disrupt means "to break or burst asunder; to break in pieces, shatter; to separate forcibly" and stems from the Latin verb *disrumpere* (Wikipedia contributors, 2020). Then, let us investigate what is shattered. Both organisms and ecosystems are composed of parts whose relations enable the whole to last over time, a property that we call organization (Nunes-Neto et al., 2014; Montévil & Mossio, 2015; Mossio et al., 2016). Disruption would then be a loss of organization, the loss or impairment of the contribution of one or several parts to an organism's or an ecosystem's ability to last over time. In a sense, it would be the opposite of the process of niche emergence described in Gatti et al. (2018). Moreover, such organizations have two analytically distinct dimensions: they form coherent, self-sustaining systems resulting from evolutionary history. We contend that a concept of disruption has to integrate both of these dimensions.

This article initiates a theoretical and conceptual work on anthropogenic biological disruptions by studying a specific phenomenon that ecologists often call disruptions. We

start with this case because there are mathematical models that we can build on, and, accordingly, it is relatively more straightforward than, for example, endocrine disruptors where development enters into the picture (Colborn et al., 1993). Let us describe this situation. Outside the equatorial zone, seasons put a steady rhythm in climates. These seasonal variations constrain living beings and their activities so that biological responses specific to it appeared in evolution. Many biological events, such as blooms, hatching, and migrations, occur at specific times of the year. The study of periodic events in the living world associated with seasonality is called phenology. Ecologists often call disruption the effect of desynchronizations on an ecosystem when they break down relations between populations (Memmott et al., 2007; Ovaskainen et al., 2013; Burkle et al., 2013b; Kudo & Cooper, 2019); these desynchronizations are also commonly referred to as phenological mismatch. They are considered a "well established" impact of climate change on ecosystems by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019b,a). Most researches focus on the description of the mechanisms of phenological mismatch (Gérard et al., 2020); however, in this article, we focus on the ecosystem level, where disruptions take place. We argue that the rationale to understand these disruptions is particular. We build on a simple model of plant-pollinator interactions to develop a mathematical framework to specify it and make explicit its difference with the concept of perturbation and the more generic concept of disturbance.

We analyze the epistemological underpinnings of models of these phenomena, that is, the way models are constructed and interpreted to generate knowledge, and we emphasize that they have remarkable characteristics in that regard, by contrast with models in physics. Our overarching thesis is that understanding these disruptions requires simultaneously analyzing i) the relations in a system and ii) the evolutionary history that originates the synchronization of the biological activities. Building on this case, we propose a formal framework that leads to new questions on the disruption of ecosystems and methods to address them. In this framework, the complete ecosystem is entirely viable only in a narrow part of the possibility space, and it is there as a result of its history. Disruptions push the system away from this part, several species disappear, and accordingly, parts of the possibility space vanish. We also use this framework and a set of empirical interaction webs to investigate whether their properties have changed in the last decades. Last, we introduce an initial, conceptual definition of biological disruptions that may apply beyond our formal framework.

2 Materials and Methods

2.1 Epistemology

Epistemology, here, is the critical study of the way scientific knowledge is constructed. A part of this article analyzes the modeling methodology and specifically the hypothesis required for models to explain the intended phenomenon. To this end, we also use methods of comparative epistemology for modeling in physics versus biology.

2.2 Data

We used plant-pollinator networks from the Web of Life database (www.web-of-life. es) and limited ourselves to their topological properties. When analyzing trends, we used at most two networks by study. Since we are interested in the time series, we consulted the original works to find data collection times. We estimated it to be two

years before publications when we could not access the reference work, or this information was not in the reference work. Besides, we excluded networks without a reference publication. The networks used are described in supplementary materials.

Since phenological data combined with local interaction networks are limited, we used the statistics of the data of Burkle et al. (2013a) to generate phenological properties of populations for other networks.

2.3 Models

New models have been implemented in R and Rcpp; details are below, in appendix A and the code is published (Code: Montévil, 2020a).

2.4 Analysis

We use the combined Nestedness metric based on the Overlap and Decreasing Fill (cNODF) measure implemented in R (Song et al., 2017, 2018). In addition, we computed network temperatures with the bipartite package (Rodríguez-Gironés & Santamaría, 2006; Dormann et al., 2008). Null models were provided by the function r2dtable of the stats package.

2.5 Statistical analysis

Cran R was used for statistical analysis. We performed mean comparisons with the base Wilcoxon rank test or with a t-test (mentioned explicitly). Statistical regressions were performed with the robust regression function of the robustbase package (Maechler et al., 2020), and we compared correlations with the cocor package (Diedenhofen & Musch, 2015).

3 Conceptual analysis of ecosystem disruption due to phenological mismatch

3.1 A paradigmatic model

Climate change impacts phenologies, the timing of seasonal activities; these disruptions are relevant economically, socially, and for conservation biology (Morellato et al., 2016; Stevenson et al., 2015). In a nutshell, if activity periods shifted coherently, typically by starting activities earlier in spring, then possible interactions would not change. However, living beings use a diversity of seasonal clues, such as air or soil temperature, snow coverage, or photoperiod (Visser et al., 2010). This diversity leads to a diversity of responses to climate change. The diversity of phenological responses leads to changes in possible interactions, and the latter can destabilize populations and ecosystems (Robbirt et al., 2014; Rafferty et al., 2015; Renner & Zohner, 2018).

For example, figure 2 represent the phenological data of (Burkle et al., 2013a). Overall, the changes lean towards activities taking place earlier, and this trend is statistically significant in the case of plants (p=0.008, t-test) and not for pollinators (p=0.24). One could hypothesize that interacting species shift coherently due to underlying adaptions, thus preserving interactions. There is a slight correlation between interacting species; however, it is not significant ($R = 0.095$, $p = 0.11$). Therefore, these data are consistent with the hypothesis that phenology changes are mostly random *with respect to*
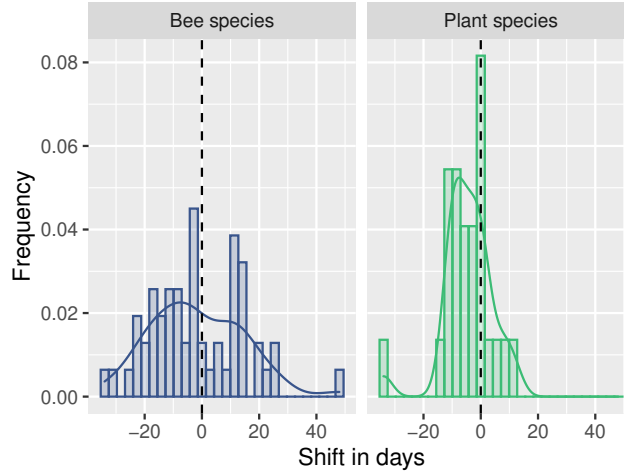
Figure 2: *Shift of plant flowering and start of bees activity in 120 years.* These graphs compare Robertson's data, collected in the late 1800s, and recent data, collected at the same location in Illinois, USA (Burkle et al., 2013a). 0 means no phenological changes; a negative change means that activity starts earlier in spring, and a positive one means that activity starts later. We emphasize that the phenological changes are diverse, leading to a change in possible interactions.

interactions — they may be seen as deterministic when considering specific physiologies; however, they can be treated statistically due to the lack of significant correlation between interacting species phenology shift.

To work out our concept of disruption, let us analyze a relatively simple model in detail. Memmott et al. (2007) modeled the disruption of plant-pollinator interactions in an ecosystem. Each plant species has a flowering period, and each pollinator has a period of activity. Their durations are considered fixed; however, climate change alters their starting time. The outcome is periods where interactions are disrupted, for example, periods where pollinators cannot feed (fig. 3). Plant-pollinator interactions stem from empirical data, specifically Robertson's data collected in Illinois at the end of the 1800s, before the significant onset of anthropogenic climate change.
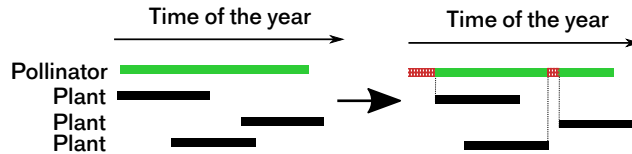
Figure 3: *Phenological change in possible interaction between a pollinator and plants due to climate, after Memmott et al. (2007).* Left: original situation. Right: situation after the change. For pollinators, the period represented is the period of activity, for the plants it is the period of flowering. In the case represented, every plant is pollinated; however, the pollinator has two periods without plants to pollinate after the change.

In this model, a significant proportion of pollinators is vulnerable to climate change. The ability to feed is disrupted in 17 to 50 % of pollinators, depending on the scenario. Specialists are particularly vulnerable because the random changes can lead to mismatches that other plants do not compensate for. Recent observations confirm this

point (Maglianesi et al., 2020). The authors do not consider that these disruptions always lead to extinction; however, they argue that they weaken the populations' ability to maintain themselves even in less damaging cases.

Let us now expand on the theoretical rationale of the model. The model is simple in that it only includes the activity periods of plants and pollinators and a fixed interaction network. Modelers assume that all plants and pollinators are initially in a viable configuration. However, viable configurations for the entire ecosystem are rare among possible activity periods because all populations need to be viable, and pollinators, especially specialists, are vulnerable to shifts in phenology. It follows that this initial configuration is in a narrow part of the possible configurations, as also shown by our model and simulation. The underlying history of these ecosystems explains this particular initial configuration.

After a period of climate change and the subsequent, diverse phenological shifts, a significant number of pollinators and some plants are no longer in a viable configuration. Here, the particular initial situation was transformed into a more random or "arbitrary" situation (with respect to viability and evolutionary history). Thus, in this model, disruption appears as the dissipation of history outcomes that impact the viability of the ecosystem's diversity (fig. 4).
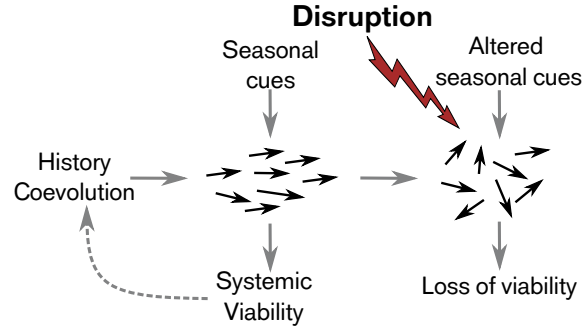

Figure 4: *Schematic of the disruption of Plant-Pollinators interactions.* Evolutionary history explains the presence of a certain, specific configuration that is associated with the system's viability. Disruption randomizes this configuration, leading to a loss of viability. The dashed arrow represents the role of viability on evolutionary time scales.

In this work, the notion of disruption builds on a specific logic. In a nutshell, this disruption model builds on two pillars: initial conditions that are specific results of evolution and interaction networks that show that the randomization of activity periods by climate change leads to a situation that is not viable for many populations.

3.2 Epistemological analysis

The above logic may seem unremarkable; however, we argue that it instantiate a fundamental departure from the reasoning on mathematical models coming from physics (see also Montévil, 2020b). Here, we argue that reasoning on history enters the picture in a precise, non-trivial mathematical manner.

To show this, we contrast classical reasoning and the one in our model of interest. In general, when analyzing a system with a mathematical model, three kinds of theoretical entities are required:

1. the structure of the relations between the system's components, such as the adjacency matrix of interactions in the example above, or more generally equations;

2. the space of possible states and the state, the latter changing due to the above relations;

3. the value of some variables, which we call here external variables, such as initial conditions or parameters. The latter are required for the model to entail predictions on state changes; however, the model does not determine their values.

There is a fundamental epistemological rule in such models. Either the values of external variables do not genuinely matter for a specific phenomenon to occur, or, on the opposite, they do matter, but then they require a supplementary explanation that the model does not give.

Let us illustrate this rule. A ball dropped in a bowl always ends immobile at the bottom. Similarly, free fall follows the same qualitative trajectory irrespective of initial conditions. In both cases, the equations describing interactions are sufficient to explain the qualitative outcome because it is the same irrespective of external variables' values. By contrast, studying a printer does not contribute much to understand how a specific printed text, such as this article, came to be. Here the value of external variables, the printer input, is critical.

In general, the structure of the relations is sufficient to explain a phenomenon if and only if the external variable's generic values lead to this phenomenon (Montévil, 2019), that is to say if external variables chosen randomly will lead to this phenomenon except possibly in rare cases. In the opposite situation, specific values of the external variables are required for the phenomenon to occur, and we need to understand how these specific values came to be in the first place.

Two debates illustrate that physicists acknowledge this question as fundamental. In cosmology, simulations show that a complex universe is possible only for a limited set of parameter values, where the parameters are the fundamental physics constants (Friederich, 2018). As illustrated above, physicists have to justify why these specific values came to be. Otherwise, some physicists provocatively revert Laplace's statement to emphasize their predicament: without a solution, they would need to hypothesize that God has chosen the parameters' "good" values. A possible explanation is that universes with all possible parameter values exist, and we exist in a universe with parameters compatible with our existence — a weak anthropic principle. This example shows that specific values for an external variable are a major concern for physicists, begging for ontologically heavy answers. Another related debate in physics pertains to entropy. Following the second principle of thermodynamics, entropy can only increase in an isolated system. Accordingly, the universe's entropy is assumed to increase over time, and the universe's initial entropy must have been lower than today. Since higher entropy means a more generic situation, the universe's initial state was a non-generic situation that requires an explanation (Rovelli, 2019).

In biology, there is a diversity of modeling situations where relations are insufficient to explain the intended phenomenon, and, instead, specific values of external variables play a critical role (Lesne & Victor, 2006; Mora & Bialek, 2011; Montévil, 2020b). Biophysicists argue that evolutionary history justifies these specific values. For example, a chromatin model leads to functional configuration only for specific values of the parameters, the equality of activation energy of two otherwise independent molecules (Lesne & Victor, 2006). The authors explicitly argue that these molecules' "coevolution" justifies the models' parameters' specific values. The paradigmatic model of plant-pollinator network disruption discussed above builds on a similar rationale, where natural history plays a fundamental role to analyze the model.

Understanding disruptions with this rationale imply that they are distinct from the concept of the perturbation of a system as defined in the mathematical methods inherited from physics — a field where history is not a fundamental theoretical concept. A perturbation is typically a small change in the state of a system used to analyze a situation's stability. For example, a population considered at equilibrium will return to its size if some individuals are added or removed (the perturbation). Attractors, used to analyze dynamics, are precisely defined as invariant by such small perturbations; they are generic outcomes. By contrast, in Memmott's model, the specific values of external parameters do not stem from the model, but their specificity and evolutionary justification play a central explanatory role. Evolutionary history is not a fundamental concept in physics, and thus it is foreign to classical perturbation analysis stemming from physics. Accordingly, disruption is an original concept with practical consequences for mathematical modeling.

In a nutshell, in the model of Memmott et al. (2007), disruption stems from the loss of specific values for external variables, the initial conditions. The underlying history justifies the initial situation's specificity. Climate change seems to randomize phenologies, and this randomness disrupts many of the initial interactions. We need now to define this randomness rigorously — provided that the phenology change for a given species may be seen as deterministic due to its specific physiology.

4 Formalism and applications

4.1 Overall rationale

To build on this epistemological discussion, let us introduce a specific method of analysis with the simplest model possible. Our analysis builds on the notion that viability is limited to a very small part of the possibility space.

We assume that, in the initial state, all populations are viable. Then climate change randomizes this state, leading to a more generic configuration, albeit one where not all populations are viable. Then, we draw the consequences of this new situation: some populations disappear. The remaining populations are again in a small part of the remaining possibility space because they are viable in this new context (the same conditions apply as before, albeit with the diminished ecosystem and the new activity periods). In a nutshell, we model disruptions in three steps: the specific initial state where all populations are viable, its randomization where the state is more generic than before, but not all populations are viable, and, last, the final configuration corresponds again to a narrow part of the remaining possibility space.

To conceptualize the randomness introduced by climate change, we build on Boltzmann's concept of entropy (Montévil, 2021). In this sense, our work is related to earlier theoretical approaches of ecology that build on entropy and information theory. For example, Ulanowicz (2009, 2019) emphasize a window of viability considering the ratio between constraints (information) and randomness at the level of ecosystems' quantitative interactions.

In our work, the viability zone is not a window but a slit in the space of activity periods — with viability conditions given by interaction networks. Moreover, we do not use the information theory but Boltzmann's schema – in particular, the latter does not require a probabilistic framework (Goldstein et al., 2020). Boltzmann starts with the notion that there are two observation levels to describe the same situation: microstates and macrostates. The basic idea is that some macrostates correspond to an overwhelmingly higher number of microstates than others. Then, if a system travels randomly

among the microstates, it tends towards these macrostates and will rarely meet the others. Then, a macrostate's entropy is just a measure of the corresponding number of microstates, and a system will tend spontaneously towards the highest entropy. We emphasize here that this rationale does not require a specific hypothesis on how the microstates change; the underlying process may be deterministic or probabilistic. As noted above, depending on the question we aim to address, it is not necessary to describe all details of the situation (Ulanowicz, 1997; Harte & Newman, 2014).

Even though we use part of Boltzmann's reasoning, we do not work with physics's entropy. Instead, we use Boltzmann's schema to analyze ecosystems' structure and changes concerning populations' activity periods. Furthermore, our approach has another specificity. Typically entropy is used to single out the most generic situation compatible with constraints and assert that the system will be in this state. In our case, instead, viability is limited to a very narrow part of the possibility space; randomness due to climate change leads to a more generic configuration; however, the latter is unstable, and the final state is again in a narrow part of the possibility space. In a nutshell, equilibrium thermodynamics goes from generic states to generic states, whereas our ecosystems go from specific states to specific states (here, in the sense of improbable).

4.2 Introducing a conceptual and formal framework

We aim to provide the simplest model to illustrate the rationale we are proposing; therefore, we greatly simplify assumptions. Figure 5 provides a summary of notations and a schematization of the rationale developed in this section.

4.2.1 The plant-pollinator model

The state of our system is the activity periods for each species of plants and pollinators. The start of each species' activity period defines a vector noted x. x is a vector of n quantities, where n is the number of species in the ecosystem. For simplicity, we assume that the activity durations do not change over time, following Memmott et al. (2007). We also assume that all individuals of populations start their activity simultaneously to simplify the model. Then, x determines the system's state. Initially, x is compatible with all species' survival; however, when the activity periods change, some populations cannot sustain themselves . We aim to analyze how random changes of x disrupt the ecosystem.

We use empirical networks from the Web of Life database, and we generate initial activity periods based on the data of Burkle et al. (2013b) and the method of Memmott et al. (2007). We define a simple model of viability. Plant survive if they are pollinated at least once by one pollinator species. Pollinators need to feed during their entire activity period with the tolerance defined by the parameter R, for robustness. Specifically, a pollinator is viable when the proportion of its activity period without a plant to pollinate is smaller than R. Agency, a, is the probability that a pollinator will feed on a new plant if it has no plant to feed on. This crude description does not estimate the specific properties of the species that constrain these changes, such as plant and pollinator morphology; nevertheless, it provides a simple account of the observed emergence of new interactions (Burkle et al., 2013b), conceptualized as a simple form of enablement (Longo et al., 2012). More details on the model are in appendix A.
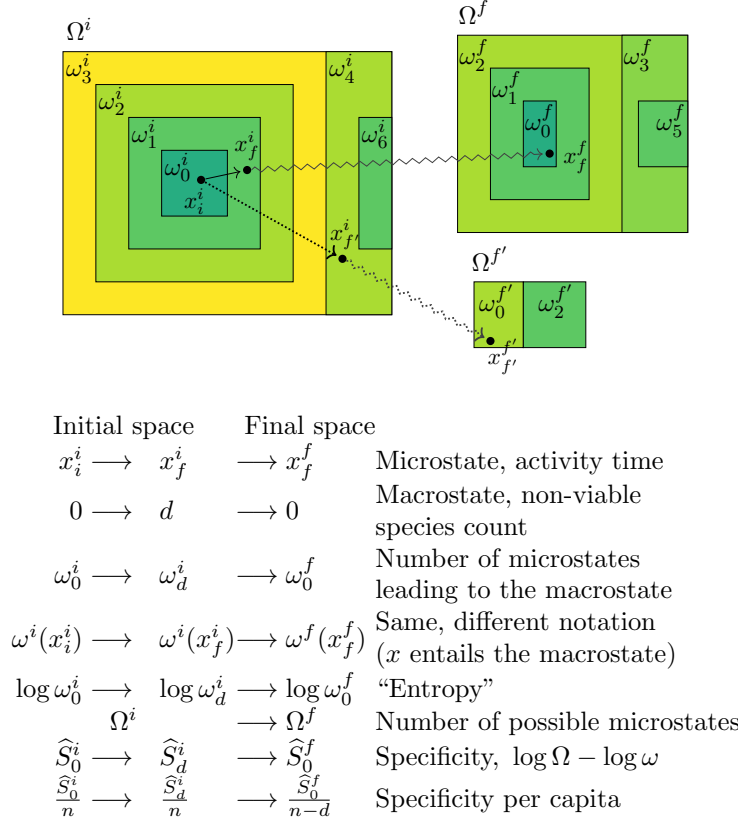
Initial space		Final space		
$x_i^i \longrightarrow$	x_f^i	$\longrightarrow x_f^f$	Microstate, activity time	
$0 \longrightarrow$	d	$\longrightarrow 0$	Macrostate, non-viable species count	
$\omega_0^i \longrightarrow$	ω_d^i	$\longrightarrow \omega_0^f$	Number of microstates leading to the macrostate	
$\omega^i(x_i^i) \longrightarrow$	$\omega^i(x_f^i) \longrightarrow$	$\omega^f(x_f^f)$	Same, different notation (x entails the macrostate)	
$\log \omega_0^i \longrightarrow$	$\log \omega_d^i \longrightarrow$	$\log \omega_0^f$	"Entropy"	
	Ω^i	$\longrightarrow \Omega^f$	Number of possible microstates	
$\widehat{S}_0^i \longrightarrow$	$\widehat{S}_d^i$	$\longrightarrow \widehat{S}_0^f$	Specificity, $\log \Omega - \log \omega$	
$\frac{\widehat{S}_0^i}{n} \longrightarrow$	$\frac{\widehat{S}_d^i}{n}$	$\longrightarrow \frac{\widehat{S}_0^f}{n-d}$	Specificity per capita	

Figure 5: *Changes in activity periods and their consequences.* The initial activity periods, x_i^i correspond to a situation where all species are viable, macrostate 0. When x changes to x_f^i, it leads to macrostate 1, where one species is not viable, and when it changes to $x_{f'}^i$ it leads to macrostate 4. In the final situation, non viable species disappear, and all remaining species are viable in the state x_f^f and $x_f^{f'}$, resp.; however, the space of possibility has changed, and there are fewer microscopic and macroscopic possibilities than initially (because there are fewer species). The representation of the microstate space corresponding to the different macrostate is indicative; the microstate size difference is far larger in a quantitative model than in this schematic representation (fig. 6). We also represented schematically the fact that going further away from x_i^i leads overall to more disappearances. However, a specific microstate region needs to be targeted to obtain more disappearance than for maximum entropy, including the extinction of the complete ecosystem (fig. 6).

4.2.2 Analysis building on Boltzmann's schema

To study plant-pollinator networks and their disruption, we posit that the microstate *sensu* Boltzmann is x, that is, the start of each species' activity period (a vector of n quantities). By contrast with physics, this vector's dimension can change because species can appear or migrate, or disappear from the ecosystem. Here we will only cover the latter case as a consequence of disruptions. It follows that when the microstate changes from the initial x_i to the final x_f, that is, when activity periods change in the ecosystem, the underlying "microscopic" space of possibility changes: the activity periods of species that disappeared are no longer relevant. This point has several ramifications.

First, we must carefully distinguish the initial state space analysis and the final state

space. We systematically indicate the space by exponent i, for initial, and f, for final. For example, x_f^i is the final microstate in the initial space. The activity periods may have changed; however, the consequences of the changes are not applied yet. Intuitively, some plants flower but cannot reproduce, and some pollinators hatch but are not viable in the ecosystem. By contrast, x_f^f is this microstate in the final space, where species that are not viable have disappeared.[1]

Second, we define the macrostates, an operation called coarse-graining. Since viability is critical to understand the system, we define the coarse-graining with it. In the initial space, we define the macrostate corresponding to the activity periods x^i by the number of species d that are not viable for this state and interaction network.[2] Then, ω_d^i is the number of microstates corresponding to situations where d species are not viable. For example, when all species are viable for the activity periods x, we are in the initial macrostate 0, corresponding to ω_0^i microstates. On the other hand, when x leads to one species not being viable, we are in initial macrostate 1, corresponding to ω_1^i configurations. Figure 6 represents the macrostates resulting from the random, equiprobable choice of microstates and the estimated corresponding number of configurations ω_d^i. Last, when x_f^i corresponds to an initial macrostate $d \geq 1$, species disappear in the final situation (n decreases). All populations that survived are compatible with the new activity periods; therefore, x_f^f corresponds to the macrostate 0 in the final space.

Third, since the space of possible microstates changes, we make its contribution explicit by the quantity Ω^i and Ω^f, the total number of possible configurations in the initial and final space, respectively. The complete space of possibility for n species is $[1, 365]^n$, thus $\Omega^i = 365^n$ and $\Omega^f = 365^{n-d} = 365^{n_f}$. Then we define the specificity :

$$\widehat{S}_d^i = \log \Omega^i - \log \omega_d^i \tag{1}$$

$$= -\log \frac{\omega_d^i}{\Omega^i} \tag{2}$$

The first term is a straightforward measure of the ecosystem biodiversity — here, it is proportional to the number of species in the ecosystem. The second term is analogous to (the opposite of) Boltzmann entropy: the higher the entropy, the more generic, or the more random the system's state is. Now, the second equality means that $\widehat{S}_d^i$ measures how specific the macrostate d is among all possible macrostates (for activity periods and viability). If Ω did not change, the specificity would be the opposite of entropy up to a constant; however, Ω changes. Figure 5 summarizes the interplay between initial and final microstates and macrostates schematically.

Here, disruption is a two steps process (Fig. 5). First, the activity periods x^i change, but the consequences of these changes do not apply yet; that is to say, we remain in the initial space. This step is critical to analyze the properties of the initial space. Second, we draw the consequences of this change; some populations may disappear and, accordingly, part of the possibility space vanishes. Crucially, only the initial macrostate 0 is compatible with sustaining the entire possibility space Ω^i. All other microstates are not genuine possibilities for this ecosystem; they are pre-possibilities as defined by Montévil (2019): states that are well defined but cannot sustain themselves in the given context. This two-step process describes an elementary disruption of a plant-pollinator ecosystem by phenological changes.

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[1]Since we are considering only disappearances, x_f^f is a projection of x_f^i on the final microspace.

[2]A finer-grained model would define macrostates by the number of plants and the number of pollinators, or even the individual species that are not viable in the ecosystem.
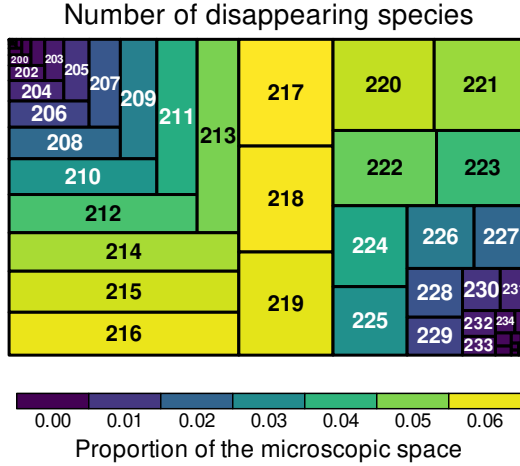
Figure 6: *Number of non viable species for random activity times. In other words, coarse-graining of microstates by the number of non-viable species.* For each macrostate d, a macrostate area is proportional to the number of corresponding microstates. We sampled the possible activity periods, i.e., the microscopic possibilities, by randomly choosing 10^7 states x. We use the network published by Kato & Miura (1996), 64 plants and 196 pollinators (260 total), with parameters $R = 0$ and $a = 0$. Overall, we observe that most microscopic states correspond to the disappearance of many species, 220 on average, that is to say, 84% (with a standard deviation of 2.5%). This result exemplifies that activity periods leading to all species' viability are in a very narrow part of the microscopic possibility space — such a state was not found by random sampling. Similarly, all species' disappearance required exploring a specific part of this possibility space and was not met randomly.

4.3 Effects of phenology changes

The space of possible activity periods is too large for an exhaustive exploration; therefore, we sample the possibilities in growing regions around the initial microscopic state x_i^i. To sample states corresponding to the complete or near-complete extinction of the ecosystem, we use the same approach; however, instead of x_i^i, we start from the situation with a shift of activity period of half a year between plants and pollinators. With this method, we estimate ω_d^i, the number of microstates corresponding to the different macrostates d.

After a change in microstate, the specificity in the initial space, $\widehat{S}_d^i$, describes how specific or, on the opposite, how generic or random the new microstate is. When specificity reaches its minimum, 0, activity periods are completely random. Figure 7A illustrates this quantity as a function of d. Specificity is the highest for macrostate 0, where all populations are viable. With increasing d, specificity decreases to a minimum that corresponds to maximum entropy. Let us recall that maximum entropy is also obtained by randomly choosing a microstate, without focusing on the neighborhood of x_i^i, as illustrated in figure 6. Above d value corresponding to maximum entropy, the specificity increases again: specific regions have to be "targeted" to entail more species' disappearance than maximum entropy macrostates. Ultimately, all species' disappearance is difficult to reach because generalists have relatively high survival chances, and, more critically, the conditions for all species to disappear after a single change is stringent.
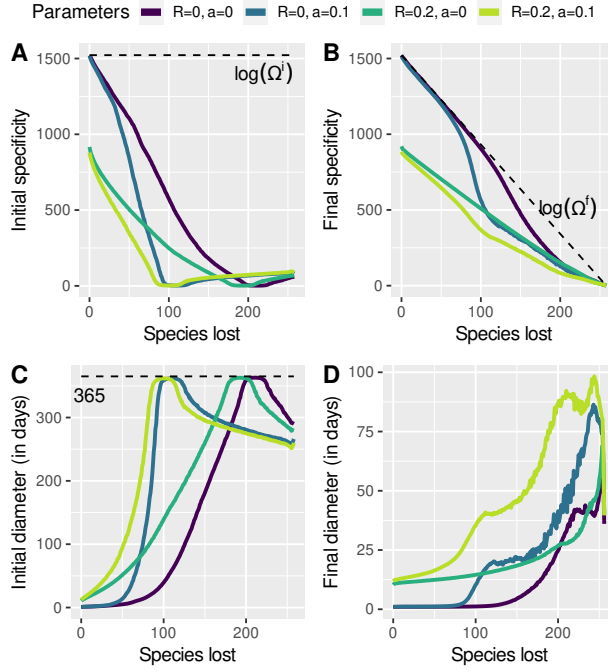
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Figure 7: *Specificity of the different macrostates (species lost).* The network stems from Kato & Miura (1996) and has 64 plants and 196 pollinators. A: the initial specificity $\widehat{S}^i_d$, the higher the specificity, the less random and the more vulnerable to disruption the macrostate is. The maximum for this quantity is $\log \Omega^i$, and is independent of d. When $R = 0$ and for $d = 0$, specificity is close to the maximum possible. B: specificity of x^f_f, that is $\log \Omega^f - \log \omega^f_0$, as a function of the macrostate of origin. This quantity describes how vulnerable to randomness the new situation is. The maximum, Ω^f, decreases linearly with the macrostate of origin, d, because d is the number of species that disappear in the process. C: similar to A, but we represent the equivalent diameter in the microscopic space in days, that is how large in days the volume of the corresponding microstates would be if they were a sphere in the microspace. Here, maximum specificity corresponds to a small diameter, while the maximum diameter, 365 days, corresponds to the minimum specificity and maximum entropy. D: equivalent diameter of w^f_0 as a function of the initial macrostate d, that is, the diameter in days of the macrostate 0 in the final space. This graph represents the robustness of the final situation. The important point is that these diameters do not reach 365 days: the system is only adapted to the new microstate and remains vulnerable to other disruptions.

There is a striking and distinct effect of the parameters. With $R = 0.2$, macrostates with few disappearances (low d) are far less specific than for $R = 0$ while the disappearances at maximum entropy are similar. By contrast, a impacts the maximum entropy configurations, $a = 0.1$ leads to less disappearance at maximum entropy than with $a = 0$.

After deriving the consequences of a microstate change, the ecosystem includes only the viable species for the new activity periods; that is, the new ecosystem is compatible with the new activity periods. However, even when the new microstate has been chosen entirely randomly, the ecosystem does not become viable for any other random states, only for this new one and other close to it. Figure 7D represents the equivalent diameter of the macrostate 0 in the final space, and we observe that this diameter does not reach

the maximum of 365. This graph represents how robust the final situation is for a new change, and the only fully robust configuration is the one where all species disappeared — it is the only configuration that further phenological changes will not impact. Our framework differs from reasoning on entropy in physics, where maximum entropy configurations are stable (in isolated systems). The entropy function describes part of the ecosystem organization: activity periods and their influence on the ecosystem's ability to sustain itself. Maximum entropy leads to extinctions, and the corresponding selection process leads to a new configuration that is no longer at maximum entropy. Note that we call the disappearance of incompatible populations a selection process even though it is distinct from the selection of variants in a population in the usual schema of population genetics. The reason is that, in these ecosystems, the criterion of survival applies to a diversity of populations. Since it removes the incompatible ones, it leads to a more specific configuration, for example, from maximum randomness in the initial space to a relatively specific configuration in the final space.

Now, the specificity change is also an interesting quantity. First the total specificity change, from x_i^i to the final situation x_f^f, that is, $\widehat{S}_0^f - \widehat{S}_0^i$, is always negative (fig. 8A,E). It corresponds primarily to the simplification of the ecosystem due to population disappearances and is close to $\widehat{S}_0^f$ represented in fig. 7B. The specificity per capita change is also interesting because it compensates for the shrinking species number. Nevertheless, this quantity remains also negative (fig. 8B,F) because the remaining populations are more robust than the initial ones — the more vulnerable species tendentially disappear first.

Total specificity is the specificity change from the initial macrostate 0 to the final macrostate 0; however, we also consider the specificity change from macrostate d to the final one, $\widehat{S}_0^f - \widehat{S}_d^i$. This quantity corresponds only to the selection process entailed by x_f, the new activity periods. This specificity change is positive, except for a very high d (fig. 8C,G). There are two reasons for this increase in specificity. First, the non-viable populations can be in many configurations, thus reducing the initial specificity, while the final macrostate requires all species to be viable, leading to a more constrained macrostate. Second, going from the initial to the final space is a selection process for a given microstate, leading to a specific set of surviving species. It is not always the same species that disappear from the macrostate d, and the final macrostate 0 corresponds to the viability of this set of interacting species. As a result, only a part of the microstates corresponding to d will remain in the final macrostate 0. There are two reasons for the very high d leading to a decrease in specificity. The initial macrostates have a high specificity — they are macrostates where the number of species that disappear is higher than for a random state. Second, the final microstate has a low specificity because many species disappeared.

Last, when comparing the curve of specificity changes of empirical networks with the ones of network stemming from a null model (fig. 8D, H), we can see that specific patterns are less pronounced and that the response is flattened. Analyzing the reason for these patterns goes beyond the scope of this article. However, we hypothesize that it may be related to structural properties such as nestedness.

In a nutshell, our framework enables us to analyze randomness at the microstate level, its impact on an ecosystem's population's viability, and the ability of robustness and resilience to counteract it. First, complete randomness, i.e., maximum entropy, does not destroy an ecosystem entirely. It only leads to a situation adapted to the new phenologies with severely reduced biodiversity. Second, specificity has decreased in the resulting situation; that is, the state becomes more generic. This property is not only a result of the decrease of the ecosystem biodiversity; it also stems from a decrease of
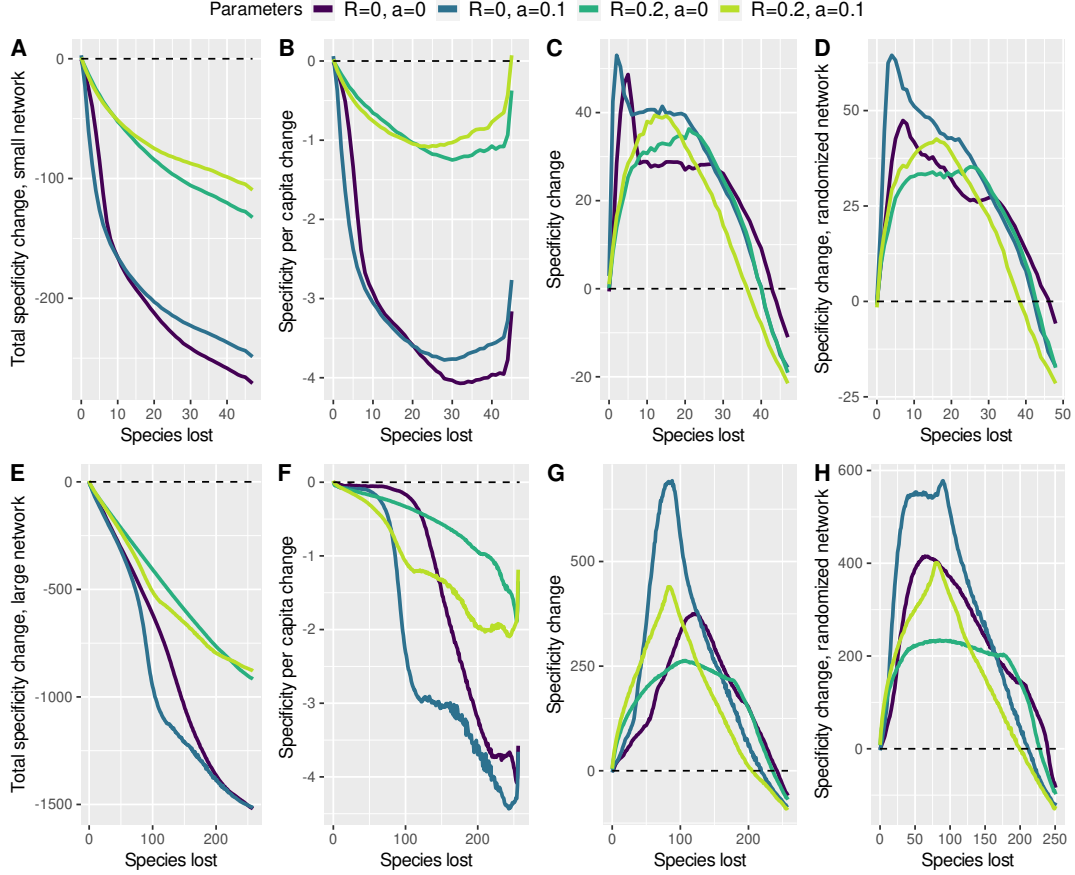
Figure 8: *Specificity change after a disruption.* Top: web published by Small (1976) with 13 plants and 35 pollinators. Bottom: web of Kato & Miura (1996) with 64 plants and 196 pollinators. A,E: Total specificity change, that is $\widehat{S}_0^f - \widehat{S}_0^i$. The change is always negative; that is, the disruption decreases specificity. Moreover, species disappearance entails a linear loss of specificity, so the decrease is close to linear. The major difference due to R stems from its effect on initial specificity (figure 7A). B,F: Specificity per species change, that is $\frac{\widehat{S}_0^f}{n_f} - \frac{\widehat{S}_0^i}{n_i}$. This quantity is also negative; however, the shrink of the possibility space no longer contributes directly. C,G: specificity change due only to applying the viability criteria, that is $\widehat{S}_0^f - \widehat{S}_d^i$. It is positive, meaning that specificity increases in the process of selection of viable populations. D,H same quantity with equivalent random webs. Random networks exhibit a flatter response than the original ones.

specificity per capita, probably due to the selection of more robust species with respect to phenology changes (generalist pollinators and plants, plants with longer activity periods, etc.). By contrast, the change from a macrostate d to the final situation leads to an increase in specificity because it is a selection process with respect to a given set of activity periods. Last, real networks show different patterns from random networks. This result suggests that our approach captures specific network properties that have been shaped by evolution.

4.4   Changes of network structure over time

We also investigate whether climate change leads to changes in interactions web that our framework can identify. To this end, we used a set of networks that biologists have collected over the years and several indicators to describe them, some standard and others based on our framework. However, joint phenology and interactions data are scarce for a given locality are scarce, and combining data from different origins will introduce randomness in our framework, which would be problematic given our purpose. Therefore, we generated phenology data by simulations.

First, we consider a property of plant-pollinator networks commonly discussed in the literature: nestedness. In nested networks, specialist pollinators interact with generalist plants and the other way around. The theoretical limitation of nestedness is that it is a purely structural property; it does not directly derive from network viability and historical construction, even though it is related to them in some models. Its relevance is therefore debated (Burgos et al., 2007; Payrató-Borràs et al., 2019). Statistical temperature is a randomness measure by contrast with a nested network, ranging from 0, perfect nestedness, to 100, a perfectly random network (Rodríguez-Gironés & Santamaría, 2006). A more accurate nestedness measure than temperature is the Nestedness metric based on Overlap and Decreasing Fill (NODF). A variation of it, cNODF, has been introduced for comparison purposes and is mostly independent of species number and connectance (Song et al., 2017). We find that network temperature increases over time ($\alpha = 0.2$, $p = 0.048$, fig. 9A). Accordingly, nestedness decreases with time ($\alpha = -0.019$, $p = 0.0015$, fig. 9B). This result strongly suggests that plant-pollinator network structures have been changing in recent years. However, we did not find an effect of ecosystems' latitude; therefore, it is not straightforward that these changes are related to phenologies (contra Song et al., 2017).

To further analyze historical trends, we used the quantities introduced by our theoretical analysis. Specifically, we investigated the proportion of species disappearing for maximum entropy configurations (fig. 9C,D) and for a realistic increase in entropy (fig. 9E,F). We use the difference between the empirical network's properties and random networks with the same dimension and marginal sums for comparison purposes. First, as a general observation, we find that the original networks always have fewer disappearing species than the average null model ones (the plotted values are negative in all but one point leading to $p < 10^{-11}$ in both cases). Real networks are more robust to random phenology changes than the null model networks.

For maximum entropy disruptions, we find an overall decrease in the number of disappearing species that does not seem linear (the trend is still significant with $p = 0.041$, with no effect of latitude). We thus separate the time window into two parts and compare them, leading to a substantial drop ($p = 0.006$, fig. 9D). This result means that networks tend to become more robust than null model networks for significant phenological changes. Therefore, we hypothesize that this result stems from the disruptions taking place in the last decades. To substantiate this claim, let us recall that we have
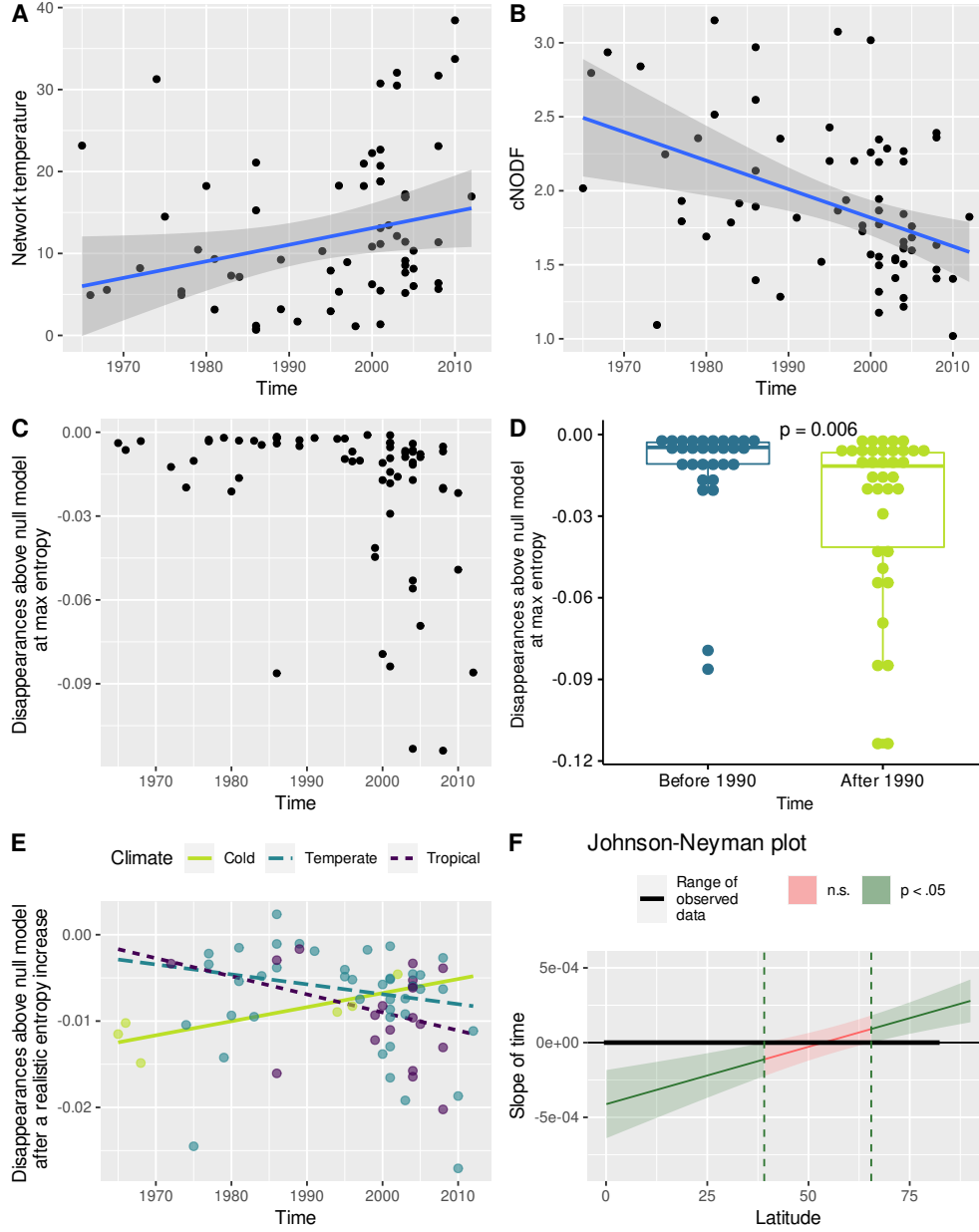
Figure 9: *Change of network properties over time.* Every point represent a network of the web of life database. A: Network temperature, an indicator opposite to nestedness, over time increases by robust regression ($p = 0.049$). B: cNODF, a nestedness indicator, decreases significantly by robust regression ($p = 0.0015$). C: disappearances above the null model at max entropy. We witness a drop in the last part of the graph, meaning that networks become more robust to complete randomization of activity periods than their null model counterparts. Parameters $R = 0$ and $a = 0.1$ D: the same variable represented by boxplot, the mean is significantly lower after 1990 than before, by a Wilcoxon rank test, $p = 0.006$. E: a lower, realistic entropy increase, represented for different latitudes, as a proxy for climates. Time, latitude, and their interaction all are significant explanatory variables. Parameters $R = 0.2$ and $a = 0.1$. F: Johnson-Neyman plot showing the effect of time depending on latitude. This plot shows for which latitude the impact of time is significantly different from 0.

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seen in examples that a disruption tends to lead to a system that is more robust to further disruptions (fig. 8B,F). We systematically compared the property plotted in figure 9D, the number of disappearances above the null model at max entropy, for networks of our dataset before and after a disruption and confirmed that networks after a disruption are more robust than before (i.e., this quantity is lower, $p < 10^{-7}$).

Concerning more realistic randomizations of the microstates, the outcome is more complex, with a significant effect of latitude, time, and their interactions. The effects are qualitatively similar and significant for all values of the parameters R and a (details are in supplementary materials). Figure 9E illustrates the time response for different latitudes, and figure 9F shows for which latitudes the estimated time response is significantly different from 0. Remarkably, the effects tend to be opposite between low and high latitude ecosystems. As above, low latitude ecosystems tend to become more robust over time than the null model, which is the expected outcome. By contrast, high latitude ecosystems lose robustness over time by comparison with the null model. This intriguing result remains to be confirmed since it is based on fewer points than the temperate and tropical trends.

In summary, there are significant changes in network structural properties over time in the database used. Moreover, indicators derived from our framework show significant changes that are consistent with its most straightforward prediction. Namely, networks that have been the object of disruptions tend to be more robust for new random changes.

5   Discussion

Let us first interpret the theoretical framework introduced above. Earth orbit has led to rhythms in terrestrial physical properties, and the latter has led to the appearance of seasonal activity periods. As a result, populations' activity periods and their synchronization became relevant aspects of ecosystems in evolution. These properties generate a considerable amount of pre-possibilities, that is, combinatorial possibilities stemming from existing properties that are not necessarily compatible with the complete ecosystem's ability to sustain itself (Montévil, 2019). The crucial point is that only an overwhelmingly narrow part of these pre-possibilities are genuine possibilities, compatible with the entire ecosystem's survival. Here, overwhelmingly narrow mean 40 over 10^{655} for one of the examples presented — let us recall that physicists estimate that there are "only" 10^{80} particles in the universe. As a result, for these aspects, the window of viability becomes so small that it is better described as a slit.

When we study an ecosystem today, it has to be in such a narrow part of the possibility space because it is the condition for the viability of its populations. However, such special configurations require an explanation. Here, the underlying reason is that ecosystems are a viable outcome of natural history. We do not mean that ecosystems are optimal, just that evolutionary history generates increasingly unlikely configurations at the ecosystems level by the evolution of their components (populations) by natural selection and the complexification of ecosystems over time (when they do complexify). Being in this narrow domain is the condition of possibility for the complete ecosystem to exist and sustain the entire possibility space (Montévil & Mossio, 2015; Gatti et al., 2018). However, climate change and the following phenological changes typically push ecosystems outside of this narrow domain. Then, part of the ecosystem disappears, and accordingly, part of this space collapses. We hypothesize that this phenomenon is a typical disruption at the ecosystem level.

Let us expand on the conceptualization of randomness in our framework. It is debatable whether phenology changes in response to climate change should be seen as

deterministic or random processes because they depend on predefined physiological and developmental properties. Building on Boltzman's rationale, we nevertheless argue that these disruptions correspond to a particular form of randomness. First, we partition the space of activity periods based on the number of non-viable populations before the phenological change's consequences are drawn. This operation defines the "macrostates". The corresponding entropy of a macrostate is the number of configurations leading to this macrostate. Then, a change in activity periods leads to a macrostate change. When this change corresponds to an entropy increase, it introduces randomness in the ecosystem. Specifically, the viability of the ecosystem's populations defines this entropy and randomness for activity periods, a fundamental, irreducible theoretical step called coarse-graining (Rovelli, 2017).

This reasoning has a very practical ramification: since viable configurations are in a very narrow part of the possibility space, a change will typically push the system towards a more generic configuration, where many populations will disappear. There is only one exception: when the change has special properties for viability; for example, if the change is the same for all populations, it does not affect viability. Similarly, we have seen that a change leading to all species' disappearance requires finding special configurations; they are not obtained entirely randomly. However, most changes are random for viability, and it is the case for the phenology changes resulting from climate change to a large extent. One may object that there may be correlations between phenology changes of interdependent species (Renner & Zohner, 2018). These correlations exist in the data we use; however, they are not significant; see discussion in section 3.1.
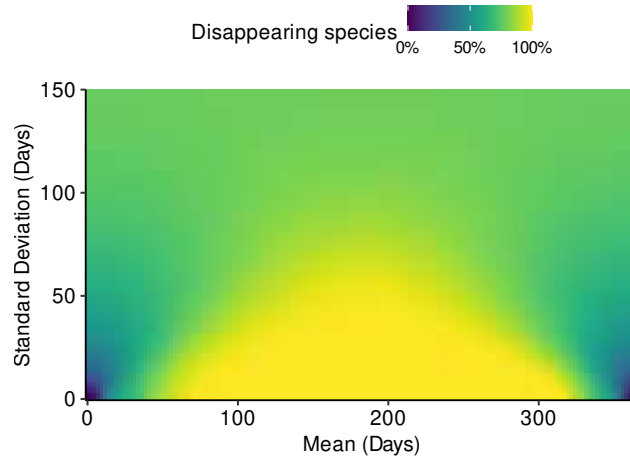

Figure 10: *Effects of Gaussian changes of activity periods.* The web stems from Kato & Miura (1996), $R = 0.2$ and $a = 0$. Gaussian random change is applied to the activity period of each species. The standard deviation is the standard deviation of activity period changes. The mean is the difference between the mean of the plant and pollinators random shifts so that a mean of 182 days means that pollinators' activity will shift of six months more than plants on average — a situation that leads to the complete extinction of the ecosystem when standard deviation is low.

As a toy example to illustrate this concept, we plotted viability as a result of Gaussian changes from the initial configuration, where the mean is the mean difference between plants and pollinators — a property that is special concerning viability (fig. 10). First, for a mean of 0, we observe that the increase of standard deviation leads to more and more disappearances up to the level of maximum entropy. Now, with 0 standard

deviation, increasing the mean leads to more and more loss of viability, that is a more and more random situation w.r. to viability, up to a point where it becomes a special change that can entail the total extinction of the ecosystem (for example, around 182 days). When the mean is high, close to 182 days, an increase in standard deviation blurs this special, detrimental change and leads to a maximum entropy configuration, where only a part of the ecosystem goes extinct. In our framework randomness is about the genericity, i.e., the lack of specificity of the macrostate, not about the process underlying microstate changes.

Analyzing anthropogenic disruptions in this framework led us to address new questions. Complete randomness for activity periods, i.e., maximum entropy, does not lead to the entire ecosystem's extinction. Moreover, robustness does not impact this outcome much; however, resilience, defined as pollinators' ability to pollinate new flowers, impacts it significantly. By contrast, robustness changes the effect of low randomization of the initial state. Moreover, we show that our measures lead to significant trends in a dataset of interaction webs for date and latitude.

Concerning theoretical principles, our approach opens new perspectives on the articulation between entropy and living systems. The entropy that we describe is conceptually distinct from physics's entropy because the latter has the physical dimension of energy by a temperature. Moreover, it accommodates the notion that entropy should be defined with respect to biological organizations and, more generally, viability (Montévil, 2021; Kauffman, 2020). We also emphasize that historicity has a double role in our reasoning. It justifies that the system is in a narrow part of the possibility space, and it also appears in the notion of changing possibility space. The latter leads to a complementary quantity to the one of entropy, based on the entire possibility space's size at a given time. This quantity is reminiscent of the concept of anti-entropy, a complementary quantity to entropy intended to describe biological complexity (Bailly & Longo, 2009; Longo & Montévil, 2012; Montévil, 2021). Additional integration between the approach developed here and the concept of anti-entropy will be the object of further work.

Let us now conclude on the concept of disruption in biology in this work. Starting from a specific result of a history that contributes to a system's viability, disruption is the randomization of this specificity leading to a less viable situation. In the case we discussed, the specific result of history entails that the ecosystem is in an extremely narrow part of the possibility space of activity periods. This situation is necessary for its complete viability, and, then, randomization leads to the disappearance of many populations. The main point is that the historical nature of biological phenomena leads to specific vulnerabilities. Disruptions explain why relatively minor temperature changes can tear apart the web of relations living beings have woven over evolutionary times. In further work, we will investigate generality of our approach by studying disruptions in different biological contexts, notably other situations in ecology and the case of endocrine disruptors in development.

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7 Statements & Declarations

7.1 Funding

7.2 Competing Interests

The author has no relevant financial or non-financial interests to disclose.

7.3 Ethics approval

Not applicable

7.4 Consent to participate

Not applicable

7.5 Consent for publication

I consent to publication.

7.6 Availability of data and material

No New data, the subset of the Web of Life database used is in supplementary materials

7.7 Code availability

The code is published here https://doi.org/10.5281/zenodo.4290494

7.8 Authors' contributions

Not applicable

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A   Models

A.1   Generation of activity periods

Initial networks stem directly from data; however, initial activity periods are not available. Therefore, we designed a small program to generate an initial configuration based

on a specific case's statistics. The relative complexity of the method stems from the fact that the initial situation is the specific result of history, as discussed in the manuscript. By random drawings, we may obtain a situation that does not accommodate the network's properties– interactions of the network need to occur–or viability conditions that we consider strictly here (without robustness).

- The time of the beginning of plant activity is selected randomly with uniform distribution with boundaries given by the data of Burkle et al. (2013a).

- The length of plant activity is obtained randomly, following a Gaussian distribution with mean and variance of the data of Burkle et al. (2013a).

- For every bee, we choose the start (resp. end) of activity periods between the earliest flowering among pollinated plants randomly and the first pollinated finishing its flowering (the earliest and the last end of pollinated plant flowering, resp.). Probabilities are the logarithm of the available pollinated plants every day. This method is inspired by Memmott et al. (2007).

- We check whether there is a gap without plants to pollinate in pollinators activity periods, in which case the pollinator is removed. We also check whether the plants are pollinated at least once.

- We check whether a sufficient proportion of the network remains after the eliminations above (threshold is 99%). If not, we draw another random situation.

A.2 Viability tests

Plants are viable when they are pollinated at least once.

Pollinators are viable if they have plants to pollinate, except at most a proportion R of their activity periods. Therefore, R represents the robustness of pollinators.

Non-viable pollinators may be "rescued" if the second parameter, a, is non-zero. Then, they have a chance $a_0 = 0.4$ of looking for flowers (i.e., plants in their activities period) that they are not interacting with and that they can interact with. More precisely, every day without a plant to pollinate and every plant, the pollinator has a chance a to establish an interaction, with $a = 0.1$ in the article's examples.

A.3 Sampling of microscopic possibility space

A.3.1 Maximum entropy

To study the effects of maximum entropy configurations, we randomly choose the start of all populations' activity periods, with uniform distribution from day 1 to day 365. Let us recall that we keep the length of activity periods constant; therefore, this process is sufficient to determine activity periods entirely. Then we record the number of species disappearances and, separately, the number of plant and pollinator disappearances.

Iterating this process leads to an estimation of the high entropy microstates' frequency, as illustrated in figure 6. For the latter illustration, we used 10^7 samples. For the time response in figure 9, we take the average for 100 times 10000 samples.

A.3.2 Realistic entropy increase

For a realistic change of activity periods, we started from the initial configuration and shifted activity periods using random samples from Gaussian distributions, one for plants and one for pollinators, with mean and variance estimated from the data of Burkle et al. (2013a). Otherwise, the logic is the same as in the previous case. For the time response in figure 9, we take the average for 100 times 10000 samples. For figure 10, we use 200 samples on every point of a 150×150 grid.

A.3.3 Systematic exploration of possibility space

Estimation of $\log(\omega_d^i)$ The number of possibilities is 365^n; therefore, exhaustive exploration is not possible. Instead, we used a multiscale approach to probe the possibility space.

More precisely, we sampled balls for $\|.\|_\infty$ (i.e., balls that are boxes) of increasing radius ρ_k centered on the initial conditions x_i^i, $B_{\rho_k}(x_i)$. We also sample balls centered on $\overline{x_i^i}$, where the plants are in the initial conditions, and pollinators' activity is shifted by 182 days to target situations where more populations disappear than in maximum entropy configurations. The balls' volume is $(2\rho_k)^n$, and we ensure that the ratio between the volume of two successive balls is larger than the sampling rate to minimize overlaps. Then,

$$\widetilde{\omega_d^i} = \sum_k \sum_{S_{B_{\rho_k}} \to d} \frac{(2\rho_k)^n}{N}$$

where $S_{B_{\rho_k}} \to d$ are the samples in ball B_{ρ_k} that correspond to the macrostate d, and N is the number of samples taken for each ball. In the graphs, we use $N = 10$ and take the mean over 200 iterations to evaluate the variables.

This method has a drawback. For example, let us consider the disappearance of a pollinator that interacts with a single plant (the latter being also otherwise pollinated). The same macrostate results from all activity periods of the pollinator that do not overlap with the plant's activity period. As a result, we include a correction term $r(d) = \sum_{i=1}^d 1/k(i)$, where $k(i)$ is the number of interactions of the pollinator i, when sorted by increasing number of interactions. This correction is heuristic and only significant for pollinators with one or two interactions, that is to say, for low values of d.

$$\log(\omega_d^i) \approx \widetilde{\log(\omega_d^i)}^{\frac{n-r(d)}{n}} + \log(365)^{r(d)}$$

Estimation of $\log(\omega_0^f)$ To estimate $\log(\omega_0^f)$ corresponding to a macrostate d, we first use the sampling method of $\log(\omega_d^i)$ to find initial microstates corresponding to d. Then, we select the ones that are representative of the largest volume of microstate. Specifically, we take the m ($m = 10$ in practice) microstates corresponding to d associated with the largest microspace volumes. Then, we assess the associated $\log(\omega_0^f)$ by taking the mean of the m estimates. Note that the web of interaction changes due to disappearances and possibly agency, so each evaluation is done with the corresponding web.

To estimate $\log(\omega_0^f)$ for a given microstate, we use the changed web as described above and the initial microstate and follow a similar scheme to estimate $\log(\omega_d^i)$. The main difference is that instead of sampling every ball, we perform a binary search for

the largest ball where all populations survive. In the paper's simulation, we take 20 samples per ball and iterate the estimation 400 times.

Supplementary Files

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- supplmentary2.pdf