

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

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## Abstract

Biologists are increasingly documenting anthropogenic disruptions, both at the organism and ecosystem levels, indicating that these disruptions are a fundamental, qualitative component of the Anthropocene. Nonetheless, the notion of disruption has yet to be theorized. Informally, disruptions are direct or indirect consequences of specific causes that impair the contribution of parts of living systems to their ability to last over time. To progress in this theorization, we work here on a particular case. Even relatively minor temperature changes can significantly impact plant-pollinator synchrony, disrupting mutualistic interaction networks. Understanding this phenomenon requires a specific rationale since models describing it use both historical and systemic reasoning. Specifically, history justifies that the ecosystem initially exists in a very narrow part of the possibility space where all its populations are viable, and the disruption leads to a more generic configuration where some populations are not viable. Building on this rationale, we develop a mathematical schema inspired by Boltzmann's entropy, apply it to this situation, and provide a technical definition of disruption.

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

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# 1 Introduction

A strategy to analyze human activities’ impact on the environment is to exhibit the sustained decline of extensive properties and derivatives, 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](#)). Similarly, ecologists focus on declining populations and decreasing species numbers – which is a subadditive count ([Leclère et al., 2020](#)). However, we assert the need for synthetic concepts to address the more qualitative anthropogenic disorganizations of the living and therefore that this rationale needs to be complemented.

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 ([Martinson & Fagan, 2014](#)), disruptions caused by climate change ([Memmott et al., 2007](#)), and endocrine disruptors ([Colborn et al., 1993](#)). 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 was theorized in the ’90s. In this sense, disruptions are new strategies transforming a market or activity structure, typically with digital technologies ([Dru, 1996](#); [Christensen](#)

et al., 2015). For example, digital platforms gathering “independent” drivers compete with taxis by bypassing the organization and regulations for both taxi and employed drivers (Dudley et al., 2017). In response, the philosopher Bernard Stiegler describes disruption at the level of human societies, arguing that today’s technological innovations are faster than societies’ ability to incorporate them through sciences, politics, customs, regulations and laws. Then, societies cannot domesticate their technological productions, leading to widespread toxic consequences for human and non-human living beings. For him, societies enter an era called “the disruption” where the problems generated by technological changes appear faster than they can be addressed (Stiegler, 2019). In this paper, we will focus on what we call elementary disruptions in biology, that is, disruptions at the level of a specific phenomenon. There is a link between the two concepts of disruptions in that the pace of elementary disruptions can be such that living beings cannot overcome them by adaptations, leading to extinctions and a decline in biodiversity — we will not address this link further in this paper.

Nevertheless, the term disruption in biology is older than in economics and philosophy. 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 affecting hormone action, Colborn et al., 1993; Gore et al., 2015). Moreover, its use grows steadily in ecology (fig. 1).

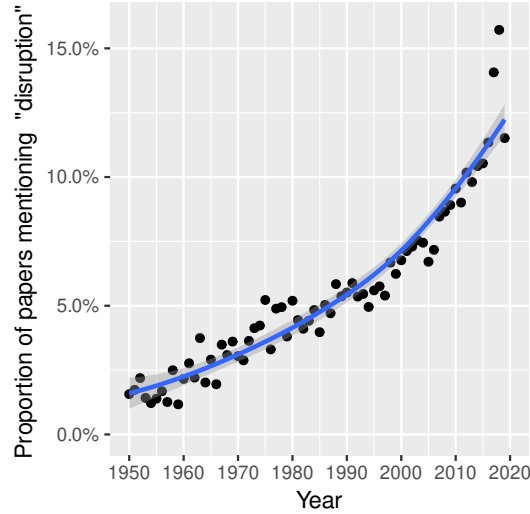


Figure 1: Occurrences of the term “disruption” and derivatives in ecology publications from 1950 to 2019. The curve represents the ratio of papers mentioning *disruption* or derivatives (*disrupt*, *disrupts* and *disrupted*) and *ecology* over papers mentioning *ecology* in the JSTOR database, in the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

In this context, theorizing disruptions will help identify biological vulnerabilities and our possible response to them. The disruptions described in biology concern a level of organization (e.g., organisms, ecosystems) and its destabilization by a specific cause (e.g., a chemical, climate change) via specific interactions (e.g., the regulation of morphogenesis, the synchrony between populations of a community). Moreover, biological disruption should be distinct from existing concepts and have theoretical specificity. Notably, it should be distinct from the familiar concept of *perturbation* coming from

physics and its root in specific mathematical methods — chiefly small perturbations around equilibrium. The latter concept is relevant to ecology and, in general, biology, where it raises specific questions (Arnoldi et al., 2016); however, disruptions should have a distinct rationale. Moreover, this concept should be relevant in diverse situations, thus possessing some generality, and accordingly contribute to explaining why disruptions are seemingly pervasive in the current biosphere.

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* (Oxford English Dictionary, July 2023). 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 (Montévil & Mossio, 2015; Mossio et al., 2016). Disruption is then 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, biological organizations have two analytically distinct dimensions: first, they form coherent, self-sustaining systems, and second, they result from history. That is to say, they are addressed scientifically by causal relations (systems) and by a reference to their past (history) (Montévil & Mossio, 2020). Let us emphasize that historicity enters biology with the theory of evolution; it does not play a role in the main theories of physics, where the objects are determined by their state at a given time and ahistorical “laws” — historicity is distinct from path dependence. We argue that a proper concept of disruption must integrate both dimensions.

This article initiates a theoretical and conceptual work on anthropogenic biological disruptions by studying a specific class of phenomena 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 the situation of interest. Earth movements put a steady rhythm in climates. These seasonal variations constrain living beings and their activities, resulting in specific biological responses 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 the break-down of relations between populations a disruption, and in line with this terminology climate change disrupts communities via phenological changes. (Memmott et al., 2007; Ovaskainen et al., 2013; Burkle et al., 2013b; Kudo & Cooper, 2019). These desynchronizations, also called phenological mismatches, lead to the decrease or disappearance of some interactions between populations for a part of the year. The impacted interactions can lead to difficulties in foraging, which are even more detrimental when associated with reproduction, for example, when birds’ eggs hatch before their prey (Both et al., 2006). They can also affect the capacity of flowering plants to reproduce sexually when the relation with pollinators is impacted (Handley & Tronstad, 2023). 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 research focuses on describing the mechanisms of phenological mismatch between the individuals of a mutualistic relationship (Gérard et al., 2020); however, this article focuses on the community level, where a specific disruption occurs. The rationale for understanding these disruptions is particular. We build on a simple model of plant-pollinator interactions to develop a mathematical framework to specify these disruptions and make explicit how they differ from the

concept of perturbation and the more generic concept of disturbance.

In this article, we analyze the epistemological underpinnings of models of these phenomena, that is, how these models are constructed and interpreted to generate knowledge. We emphasize that they have remarkable characteristics when compared 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 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 in such a configuration due to its history. Disruptions push the system away from this part, several species disappear, and, accordingly, parts of the possibility space vanish. Plasticity and variability can partly compensate this disruption; however, the extent of this compensation is limited. We also use this framework and empirical ecological networks to investigate whether the last decades impacted network properties. Last, we introduce a conceptual definition of biological disruption that is applicable beyond our formal framework.

## 2 Data and Methods

### 2.1 Epistemology

Epistemology is the critical study of how scientific knowledge is constructed. A part of this article analyzes the mathematical conditions for a model to explain the intended phenomenon; that is, which mathematical hypotheses are required to entail which consequences. To this end, we also use methods of comparative epistemology for modeling in physics versus biology. Specifically, we focus on the singularity of models of disruptions. We also discuss the concept of randomness as it is essential to our theoretical construction.

### 2.2 Data

To evaluate the trend in the use of the term disruption, we use JSTOR’s database because of its accessibility and interdisciplinary coverage. The results are also more consistent than those of Google Scholar, which is not designed for this purpose.

We used plant-pollinator networks from the Web of Life database (<https://www.web-of-life.es>) and limited ourselves to their topological properties. When analyzing historical trends, we used at most two networks by study to limit its statistical weight; otherwise, a study with many networks would dominate the statistical analysis. Since we are interested in the historical trends in plant-pollinator networks, we consulted the original works to find data collection times. We estimated the observation time to be two years before publications when we could not access the reference work or when this information was not in the reference work. Besides, we excluded networks without a reference publication. The 69 networks used are described in supplementary materials.

Since phenological data combined with local interaction networks are extremely limited, we used the statistics of the data of [Burkle et al. \(2013a\)](#) to generate simulated phenological properties of populations with the method described in appendix [A.2](#).

### 2.3 Models and analysis

New models and the corresponding analysis have been implemented in R and Rcpp; details are in section [4](#), in appendix [A](#), and the code is published (Code: [Montévil](#),

2020).

Moreover, we use two common indicators of network topologies to analyze network changes due to disruptions. We used the combined Nestedness metric based on the Overlap and Decreasing Fill (cNODF) measure implemented in R (Song et al., 2017, 2018). We also 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, meaning that the marginal totals are kept constant or, in biological terms, that the number of pollinator populations for each plant and the number of plant population for each pollinator are kept constant.

## 2.4 Statistical analysis

Cran R was used for statistical analysis. We performed comparisons with the base Wilcoxon rank test or a t-test (mentioned explicitly). Statistical regressions were performed with the robust regression function of the `robustbase` package (Maechler et al., 2020), that is to say, the MM-estimation method, which is more robust to outliers than traditional least square regression (Koller & Stahel, 2011). We mainly performed regression to assess historical trends in the networks available in the Web of Life database over time and also considered the effect of latitude. The underlying hypothesis is that the more recent networks have already been subjected to disruptions and should have a distinct structure. Possible confounding factors, such as the context of the studies, are left for further study. Overall, we take  $p < 0.05$  as the statistical significance threshold.

# 3 Conceptual analysis of ecosystem disruptions due to phenological mismatch

## 3.1 A paradigmatic model

Climate change impacts phenologies, that is, the timing of seasonal activities. If activity periods shifted coherently, typically by starting activities earlier in spring, then possible interactions would not change. However, living beings use diverse seasonal clues (Zeitgeber), 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). These disruptions are relevant economically, socially, and for conservation biology (Morellato et al., 2016; Stevenson et al., 2015).

For example, figure 2 represents the phenological data of Burkle et al. (2013a). Overall, the changes between the phenological data of Robertson, from the late XIXth century, and data collected in 2009/2010 show a trend towards activities taking place earlier in the calendar year, and this trend is statistically significant in the case of plants ( $p = 0.008$ , t-test) but not for pollinators ( $p = 0.24$ ). An extensive study of European pollinators found that pollinators start their flight earlier on average than 60 years ago, that the shifts correlate with phylogeny, but also emphasizes the diversity in changes (Duchenne et al., 2020). One could hypothesize that interacting species shift coherently due to underlying adaptations, thus preserving interactions. In the Burkle et al. (2013a) data, 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, at least for the most part, random *with respect to*

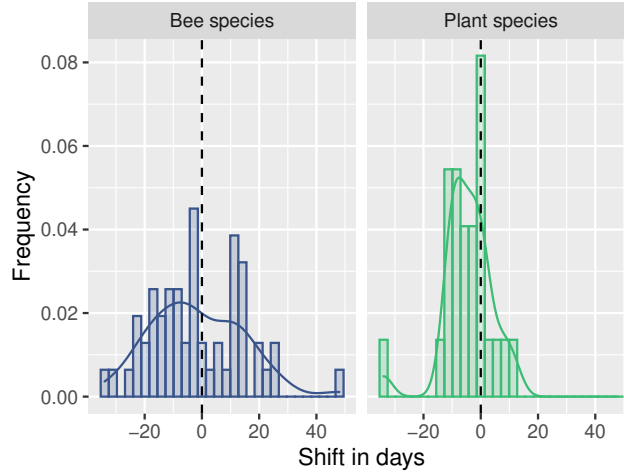


Figure 2: *Shift of plant flowering and the start of pollinator activity in 120 years.* These graphs compare Robertson’s data, collected in the late 1800s, and recent data, collected at the same location in Illinois, USA (Burkle et al., 2013a). 0 means no phenological changes; a negative change means 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 because an important part of the change does not follow a correlation between the phenology shift of interacting species.

Let us expand on this point. Here, we can describe the situation as a randomization with respect to interactions in a similar way to the concept that mutations are random with respect to fitness (Mayr, 1961). As mentioned before, the shifts of individual populations can be analyzed in detail to unravel their determinants; however, these shifts, or at least a significant component of them, are not biased to maintain interactions. This notion is compatible with the average of the shift leading to earlier activities of plants and pollinators: this average is not a contribution to this randomization, and crucially, it does not change possible interactions. Interactions are changed when interacting species phenologies change in diverse ways, which is why a disruption occurs.

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 population has a flowering period, and each pollinator population 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 initial 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.

In this model, many pollinators are 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). In Memmott et al. (2007), the authors do not consider that these disruptions always lead to extinction; however, they argue that they weaken the populations’ ability



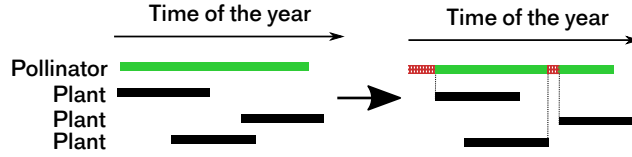


Figure 3: *Phenological change in possible interaction between a pollinator population and plants due to climate change, after Memmott et al. (2007).* Left: original situation. Right: the situation after the change. For pollinators, the period represented is the period of activity in green; for the plants, it is the period of flowering in black. In the case represented, every plant is pollinated; however, the pollinator has two periods without plants to pollinate after the change, in dotted red.

to maintain themselves even in less damaging cases.

Let us now expand on the theoretical rationale of the model. 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. Of course, plasticity, such as possible alternative food sources for pollinators, for example, would broaden the zone of viability, though at the cost of the pollination function. The point is that plant flowering and pollinator hatching are irreversible events for which there is no a posteriori flexibility. 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 randomization of history outcomes that impacts the viability of the ecosystem’s diversity (fig. 4). In other words, the situation becomes more generic than before the disruption because its qualitative properties correspond to a larger subset of possible configurations.

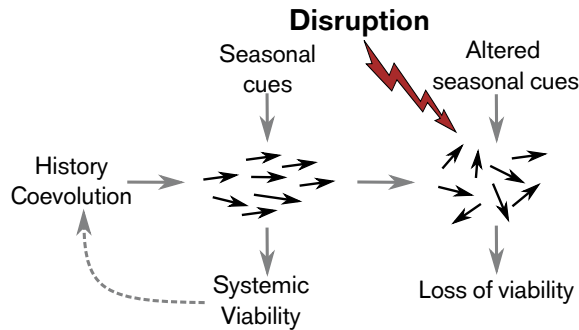


Figure 4: *Schematic of the disruption of plant-pollinator interactions.* Evolutionary history explains the presence of a specific configuration associated with the system’s viability. Disruption randomizes this configuration, leading to a loss of viability. The dashed arrow represents the role of viability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



In this work, the notion of disruption builds on a specific logic. In a nutshell, the 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 to one or more of the populations of the interaction network. In other words, climate change and the subsequent changes in phenologies push the system outside the narrow zone where all populations are viable, in favor of a more generic situation where fewer populations are viable.

### 3.2 Epistemological analysis

The above logic may seem unremarkable; however, we argue that it instantiates a fundamental departure from the reasoning on mathematical models coming from physics (see also [Montévil, 2022](#)). 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 model by [Mommott et al. \(2007\)](#), or more generally, equations;
2. the state and the space of possible states. The state is a point in the latter and changes due to the above relations;
3. the values of some variables, which we call external variables, such as initial conditions or parameters. The latter are required for the model to predict state changes; however, the model does not determine their values.

Jointly, the space of possible states and the space of the possible values of the external variables form the possibility space, see [Robert & Montévil \(submitted\)](#) for a longer discussion.

There is a fundamental epistemological rule in such models. Either the values of external variables do not genuinely matter for a qualitative, specific phenomenon to occur. In this case, the knowledge of the relations is enough to explain the phenomenon. By contrast, specific values of the external variables may be required. Then, the latter requires 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 contributes little to understanding how a specific printed text, such as this article, came to be. Here, the value of external variables, the printer input, is critical. The same applies to a specific DNA sequence of a living being: the DNA molecule may very well have been constructed by the enzymes involved in replication; however, the study of the generic replication process is insufficient to understand how this specific molecule came to be.

In general, the structure of the relations is sufficient to explain a phenomenon if and only if the external variables’ generic values lead to this phenomenon ([Montévil, 2019](#)), that is 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 invert 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 external variables constitute a significant concern for physicists, begging for ontologically heavy answers — God or multiple universes. 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, 2022). 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 acknowledge the difficulty and explicitly argue that these molecules’ “coevolution” justifies the model 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 when analyzing the model.

Understanding disruptions with this rationale implies 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; thus, it is foreign to classical perturbation analysis stemming from physics. Accordingly, disruption is an original concept with practical consequences for mathematical modeling.

A possible objection would be that we can recover a generic understanding of the situation by coupling the ecological model with an evolutionary model without appealing to specific values of parameters and initial conditions. We agree that such models can be produced; however, this approach has two caveats. First, the models will typically not generate the specific ecosystems observed since evolutionary models typically include a significant amount of randomness — unless some teleological element is introduced, which would ruin the quality of the model. Second, and more importantly, the models will come with many hypotheses that will be more or less justifiable and specific,

whereas the reasoning above remains the same irrespective of evolutionary details: it has greater generality. Of course, the two perspectives can complement each other well to understand the phenomenon better.

In a nutshell, in the model of [Mommott 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. In other words, why would disruptions take place? Because evolution leads to situations that are viable for only a small part of the possibility space, and the cause of the disruption pushes the system toward a more generic, less viable situation because it is random with respect to viability. We need now to define this process rigorously — provided that the phenology change for a given species may be seen as deterministic due to its specific physiology.

## 4 Analytic scheme and applications

### 4.1 Overall rationale

To build on this epistemological discussion, let us introduce a specific analysis method with a simple model of plant-pollinator relationship disruption by climate change. We build on the notion that viability is limited to a very small part of the possibility space.

We assume that, in the initial state that is given by activity periods, all populations are viable. Then climate change randomizes the activity periods, 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 viability criteria apply as before, so the reduced ecosystem is again in a small part of the remaining possibility space). In a nutshell, we model the situation 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, which 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, 2023](#)). In this sense, our work is related to earlier theoretical approaches to ecology that build on entropy and information theory. For example, [Ulanowicz \(2009, 2019\)](#) emphasize a window of viability determined by constraints (information) and randomness at the level of ecosystems’ quantitative interactions. In our work, the viability zone is not genuinely a window but a very small subset of 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. Some macrostates correspond to an overwhelmingly higher number of microstates than others. Then, if a system is displaced 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’s entropy tends to increase. 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 unnecessary to describe all the situation’s details (Ulanowicz, 1997; Harte & Newman, 2014). In other words, the Boltzmann schema enables us to discuss how generic or, on the contrary, how special a given microscopic situation is with respect to the properties defining the macrostates.

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. Specifically, for plants and pollinators, we choose the activity periods of all populations as the microstate, and the macrostate is defined by the viability of these population – more details are given below. Furthermore, our approach has another specificity. Typically, entropy is used to single out the most generic situation compatible with constraints and to 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; randomization 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 more or less generic states to the most generic states. In contrast, our ecosystems go from specific states to specific states (here, in the sense of a small part of the microspace).

## 4.2 Introducing a conceptual and mathematical framework

We aim to provide the simplest model to illustrate the rationale we are proposing; therefore, we greatly simplify assumptions. Figure 5 summarizes notations and schematizes the rationale developed in this section.

### 4.2.1 The plant-pollinator model

The state of our system aims to describe the seasonal activity periods for each species of plant and pollinator and we assume that there is only one seasonal activity period per population, that can be described by its starting and stopping day. Specifically, the day of the start of each population’s activity period defines a vector noted  $x$  in  $[1, 365]^n$ .  $x$  is a vector of  $n$  quantities, where  $n$  is the number of species in the ecosystem. We assume that there is no migration, thus  $n$  can only decrease due to disappearance. For simplicity, we assume that the activity durations do not change over time, following Memmott et al. (2007), and they are therefore parameters of the model. We also assume that all individuals of a population start their activity simultaneously to simplify the model. Then,  $x$  determines the activity periods of all populations and thus the system’s state. Initially,  $x$  is compatible with all species’ survival; however, some populations cannot sustain themselves when the activity periods change, that is, in terms of our assumptions, when the starting day of these periods change. We aim to analyze how random changes of  $x$  disrupt the ecosystem.

We use empirical networks from the Web of Life database and 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 for a given matrix of interaction  $M$ . Plants survive if their flowering time overlaps at least one day with the activity of one pollinator population they can interact with according to  $M$  — we neglect vegetative reproduction. Pollinators need to feed on an active plant they can interact with according to  $M$  every day of their 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  $R$ .

To account for the plasticity and flexibility of ecological interactions; we also introduced a parameter  $a$ , for agency.  $a$  is the probability that a pollinator that has no plant

to feed on will feed on a plant it used to ignore and that is flowering. In this case, an element of the interaction matrix will change from 0 to 1 due to the new interaction. Here, we do not take into account the specific properties of the species that constrain the possibility of such a change in interactions, such as plant and pollinator morphology; nevertheless, this parameter provides a straightforward account of the observed emergence of new interactions, that is, pollinators foraging on a new plant population (Burkle et al., 2013b), conceptualized as a simple form of enablement (Longo et al., 2012).

Since the model only describes populations and not individuals, it does not account for the robustness provided by intra-population variability, notably variability in phenology, that is to say starting time of activity periods and their durations. Nevertheless, the robustness parameter is a proxy for this variability since it introduces margins of tolerance for pollinators. More details on the model are in appendix A.

#### 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  $x$ , the start of each species’ activity period (a vector of  $n$  quantities). This vector’s dimension can change because species can appear, migrate, or disappear from the ecosystem. Here, we will only cover the latter case as a consequence of disruptions. When the starting moments of species’ activity periods in the ecosystem change in going from the initial microstate  $x_i$  to the final microstate  $x_f$ , the underlying “microscopic” space of possibilities changes as well: the activity periods of species that disappeared are no longer defined. This point has several ramifications.

First, we must carefully distinguish the analyses in the initial state space and the final state space. We systematically indicate the space by the superscript  $i$  for the initial and  $f$  for the final state space – the subscript indicates the initial (resp. final) state. For example, in the analysis  $x_i^i$  becomes  $x_f^i$ , the final microstate in the initial space, and then  $x_f^f$  the final microstate in the final space. For  $x_f^i$ , the activity periods may have changed; however, the consequences of the changes have not yet been applied. Intuitively, some plants flower but cannot reproduce, and some pollinators hatch but are not viable in the ecosystem. By contrast,  $x_f^f$  is the final microstate in the final space, where species that are not viable have disappeared.<sup>1</sup>

Second, we define the macrostates, an operation called coarse-graining. Since viability is critical to understanding the system, we define the coarse-graining on the basis of this criterion. In the initial space, we define the macrostate corresponding to any activity periods  $x^i$  by the number of species  $d$  that are not viable for this state and interaction network, without specifying these species.<sup>2</sup> Then,  $\omega_d^i$  (resp.  $\omega_d^f$ ) is the number of all microstates corresponding to situations where  $d$  species are not viable in the initial (resp. final) space. For example, when all species are viable for the activity periods referred to in  $x$ , we are in the initial macrostate 0, corresponding to  $\omega_0^i$  microstates. On the other hand, when  $x$  implies that one species is not being viable, we are in initial macrostate 1, corresponding to  $\omega_1^i$  configurations. Figure 6A represents the macrostates resulting from the random, equiprobable choice of microstates and the estimated corresponding number of configurations  $\omega_d^i$ . Last, when  $x_f^i$  corresponds to an initial macrostate  $d \geq 1$ , species disappear in the final situation ( $n$  decreases). All surviving populations are

<sup>1</sup>Since we are considering only disappearances,  $x_f^i$  is a projection of  $x_f^i$  on the final microspace.

<sup>2</sup>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.

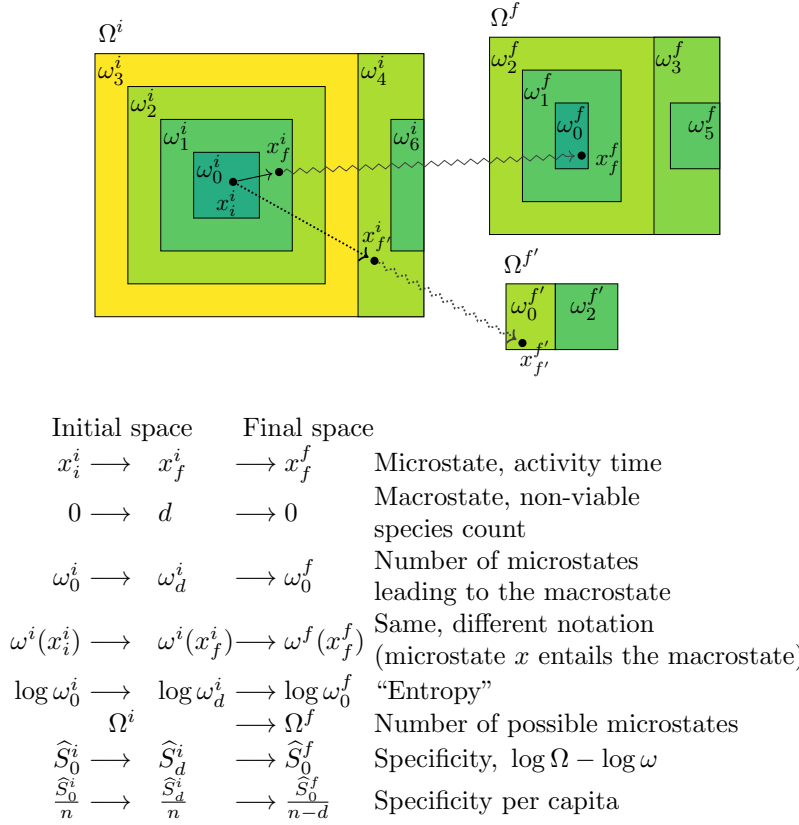


Figure 5: *Changes in activity periods and their consequences.* The colors correspond to macrostates' entropy. The arrows illustrate two alternative changes in microstate and their consequences. The initial activity periods  $x_i^i$  correspond to a situation where all species are viable, macrostate 0. When  $x$  changes to  $x_f^i$ , it leads to macrostate 1, where one species is not viable, and when it changes to  $x_f^f$ , 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 possibility space has changed, and there are less 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 schematically represented that going further away from  $x_i^i$  leads to more disappearances till maximum entropy is reached for the largest volume,  $d = 3$  here. Moreover, a specific microstate region needs to be targeted to obtain more disappearances than for maximum entropy, including the extinction of the complete ecosystem. We represented this point: the area of the region as a function of the number of disappearing species increases to a maximum and then decreases (fig. 6).

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 quantities  $\Omega^i$  and  $\Omega^f$ , the total number of possible configurations in the initial and final space, respectively. The complete space of possibilities 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:



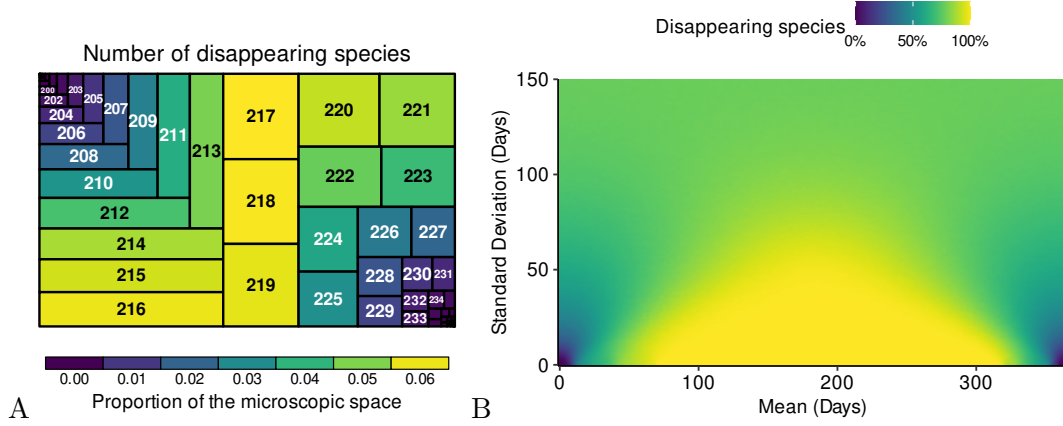


Figure 6: *Two randomizations and their consequences.* We use the network published by [Kato & Miura \(1996\)](#), 64 plants and 196 pollinators (260 total). A: We sampled uniformly the possible activity periods, i.e., the microscopic possibilities, by randomly choosing  $10^7$  states  $x$ . For each macrostate  $d$ , the number of corresponding microstates defines the represented macrostate area. Overall, we observe that all sampled 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. Simulations performed with  $R = 0$  and  $a = 0$ . B: Starting from viable conditions, Gaussian random changes are 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. A mean of 182 days means that pollinators' activity will shift six months more than plants on average, leading to complete ecosystem extinction when the standard deviation is low. Simulations performed with  $R = 0.2$  and  $a = 0$ .

$$\hat{S}_d^i = \log \Omega^i - \log \omega_d^i \quad (1)$$

$$= -\log \frac{\omega_d^i}{\Omega^i} \quad (2)$$

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  $\hat{S}_d^i$  measures how specific the macrostate  $d$  is among all possible macrostates (for activity periods and viability). If  $\Omega$  did not change, the specificity would be the opposite of entropy up to a constant; however,  $\Omega$  changes.  $\log$  refers to the natural logarithm in our numeric applications. Figure 5 summarizes the interplay between initial and final microstates and macrostates schematically.

The specificity is also a measure of the system's vulnerability to a shift in its microstate. The higher the specificity, especially of macrostate 0, the smaller the viability domain is. Considering that all quantities stem from logarithms, high specificity means that the domain of viability is extremely small and that history is required to explain



why it is observed in the first place. As illustrated by Figure 6A, the macrostate 0 is not obtainable by random sampling.

Let us also emphasize that high specificity when  $R$  and  $a$  are not null means that robustness and agency can only slightly compensate for shifts in phenologies. In particular, the variability w.r.t. activity periods indirectly addressed by  $R$  are insufficient to compensate for the fine-tuning required for viability. A reason for this is that flowering and the start of pollinator activity are events whose timing cannot be adjusted once they happen.

In brief, disruption is a two-step 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  $\Omega^i$ . 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.

### 4.3 Effects of phenology changes

The space of possible activity periods is too large for an exhaustive exploration. Figure 6A illustrates that uniform random sampling does not detect most macrostates due to their specificity. Accordingly, it displays the states with the highest entropy and this state correspond to a high number of disappearances but not a complete extinction of the ecosystem. Another approach is to start from the initial situation and to shift it by a Gaussian random vector. We plotted the subsequent viability, where the standard deviation is the usual Gaussian standard deviation. However, the mean is the mean difference between plants and pollinators — a special property, i.e., not random, with respect to viability (fig. 6B). First, for a mean of 0, we observe that the increase in standard deviation leads to more and more disappearances up to the level of maximum entropy. Now, in the limit case of standard deviations 0, the change is deterministic. Then, increasing the mean shift of pollinator w.r. to plants leads to more and more disappearances, that is, a more and more random situation w.r.t. 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. It 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.

For systematic assessments, we sample the possibilities in increased 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  $\omega_d^i$ , the number of microstates corresponding to the different macrostates  $d$ .

After a change in microstate, the specificity in the initial space (resp. final space),  $\hat{S}_d^i$  (resp.  $\hat{S}_d^f$ ), describes how specific or, on the opposite, how generic (or random) the new microstate is. When specificity reaches its minimum, 0, activity periods are entirely random. Figure 7A illustrates this quantity as a function of  $d$ . Specificity

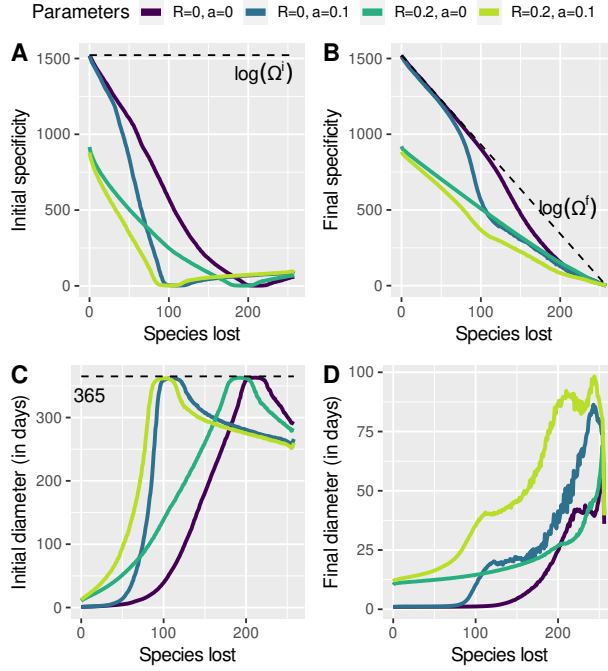


Figure 7: *Specificity of the different macrostates (species lost)*. The network stems from [Kato & Miura \(1996\)](#) and has 64 plants and 196 pollinators. A: the initial specificity  $\hat{S}_d^i$ , the higher the specificity, the less random and the more vulnerable to disruption the macrostate is. 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  $\log \Omega^f - \log \omega_0^f$ , as a function of the macrostate of origin. This quantity describes how vulnerable the new situation is to randomness. The maximum,  $\Omega^f$ , decreases linearly with the macrostate of origin,  $d$ , because  $d$  is the number of species that disappear. C: similar to A, but we represent the equivalent diameter in the microscopic space in days. This indicates the diameter of a sphere in microspace with the same volume. 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  $w_0^f$  as a function of the initial macrostate  $d$ , here 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 of the same kind.

is the highest for macrostate 0, where all populations are viable. With increasing  $d$ , specificity decreases to a minimum corresponding 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 6A. Above a value for  $d$  corresponding to maximum entropy, the specificity increases again: specific regions have to be "targeted" to entail a higher number of disappearances than is required for maximum entropy macrostates. Ultimately, generalists have relatively high chances of survival; thus, the disappearance of all species is difficult to reach.

The parameters have striking and distinct effects. 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 others close to it. Figure 7D illustrates the equivalent diameter of macrostate 0 in the final space; specifically, this is the diameter of a sphere with the same volume as the corresponding microstates. 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 its 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 survival criterion applies to diverse 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,  $\hat{S}_0^f - \hat{S}_0^i$ , is always negative (fig. 8A,E). It corresponds primarily to the simplification of the ecosystem due to population disappearances and is close to  $\hat{S}_0^f$  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,  $\hat{S}_0^f - \hat{S}_d^i$ . 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). This increase in specificity comes from straightforward reasons. The non-viable populations can be in many configurations, thus reducing the initial specificity. At the same time, the final macrostate requires all species to be viable, leading to a more specific macrostate. When  $d$  is high, other considerations explain the decreased 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 mostly generalists remain.

Last, when comparing the curve of specificity changes of empirical networks with the ones of networks 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, defined as a change independent of viability at the microstate level, its impact on an ecosystem's population's viability, and the ability of robustness and resilience to counteract it. First,

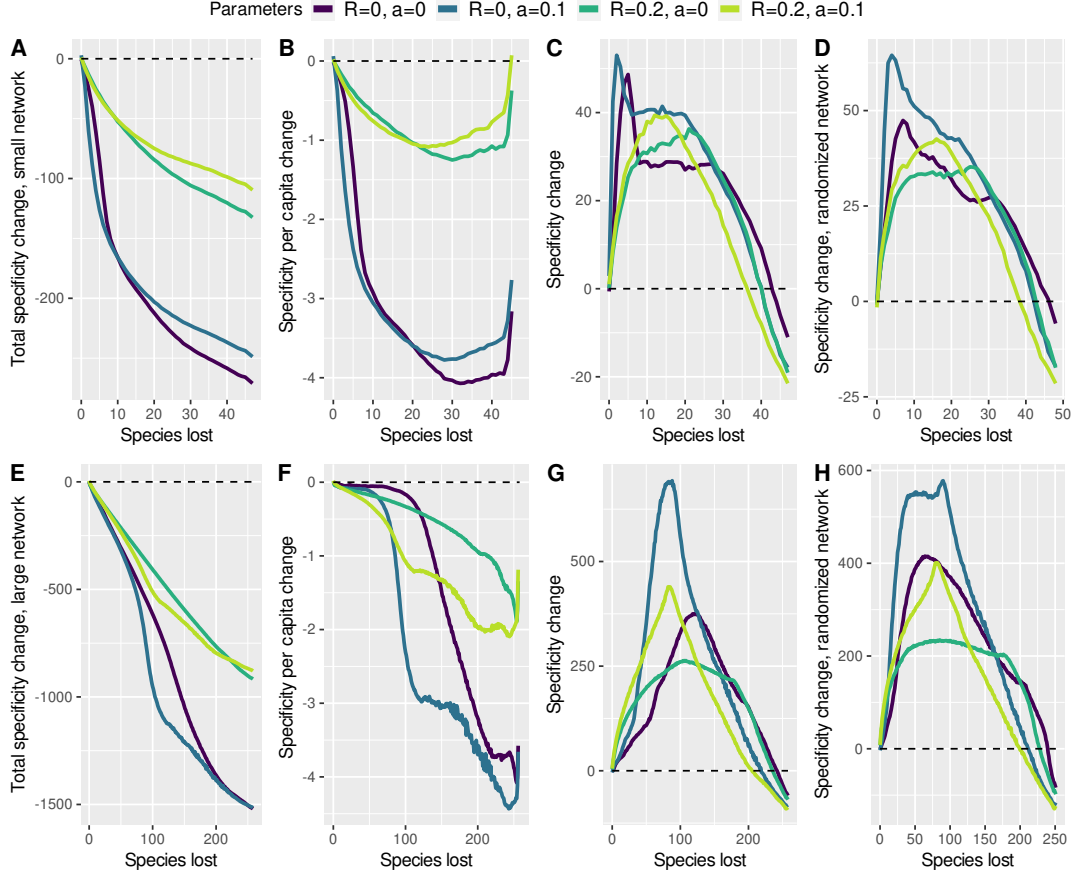


Figure 8: *Specificity change after a disruption*. Top: web published by [Small \(1976\)](#) with 13 plants and 35 pollinators. Bottom: web of [Kato & Miura \(1996\)](#) with 64 plants and 196 pollinators. A,E: Total specificity change, that is  $\hat{S}_0^f - \hat{S}_0^i$ . The change is always negative; that is, the disruption decreases specificity. Moreover, species disappearance entails a linear loss of specificity, so the decrease has a linear component. The major difference due to  $R$  stems from its effect on initial specificity (figure 7A). B,F: Specificity per species change, that is  $\frac{\hat{S}_0^f}{n_f} - \frac{\hat{S}_0^i}{n_i}$ . 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  $\hat{S}_0^f - \hat{S}_d^i$ . 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.

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 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 increases 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 shaped by history.

#### 4.4 Changes of network structure over time

We also investigate whether climate change leads to changes in interaction networks 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 interaction data are scarce for a given locality, and combining data from different origins will introduce noise in our framework. Therefore, we generated phenology data by simulations (see appendix A.2).

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 vice versa. 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 with respect to a nested network, ranging from 0, perfect nestedness, to 100, a perfectly random network (Rodríguez-Gironés & Santamaría, 2006). The Nestedness metric based on Overlap and Decreasing Fill (NODF) is a more accurate nestedness measure than temperature. A variation of it, cNODF, has been introduced for comparison purposes and is mostly independent of species number and connectance (Song et al., 2017). Network temperature increases over time (estimate of the slope of the regression line  $\alpha = 0.2$ ,  $p = 0.049$ , fig. 9A). Accordingly, nestedness decreases with time ( $\alpha = -0.019$ ,  $p = 0.0015$ , fig. 9B). This result suggests that plant-pollinator network structures have changed 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). Moreover, the differences in sampling method can impact network topology and be a confounding factor (Dunne, 2006).

We used the quantities introduced by our theoretical analysis to analyze historical trends further. 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; that is, networks of the same size and where the number of interaction of plant and pollinators are the same. 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, which we hypothesize results from the underlying evolutionary process, a result similar

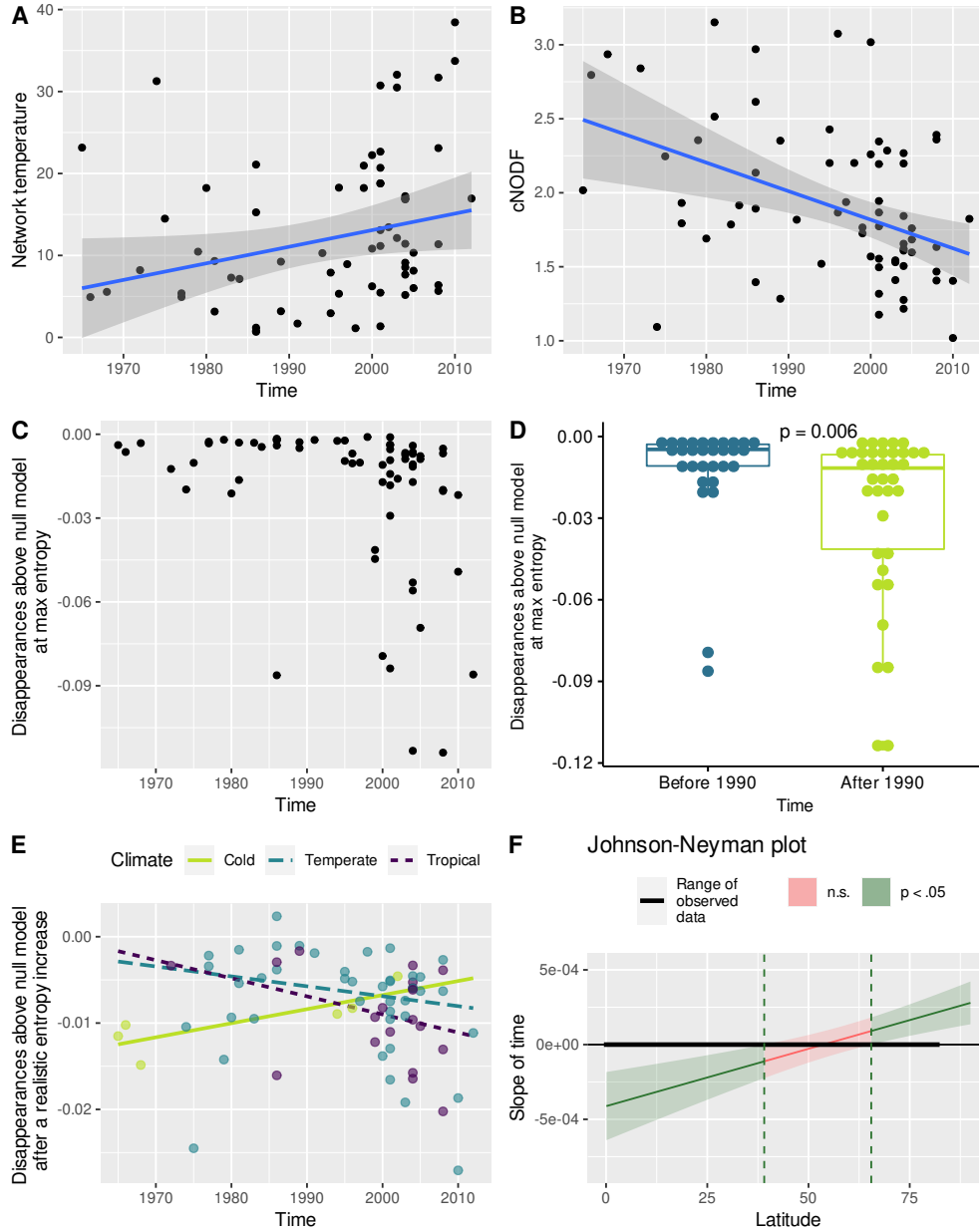


Figure 9: *Change of network properties over time.* Every point represents a network of the Web of Life database. A: Network temperature, an indicator opposite to nestedness, over time increases by robust regression ( $p = 0.049$ ). B: cNODF, a nestedness indicator, decreases significantly by robust 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 median 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 are all 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 on disappearances significantly differs from 0.



to observations in section 4.3.

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 seen in examples that a disruption tends to lead to more robustness 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 mentioned 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, the database used shows significant changes in network structural properties over time. 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 to new random changes.

## 5 Conclusion

Let us first interpret the theoretical framework introduced above. Earth’s orbit has led to rhythms in terrestrial physical properties, and the latter have led to the appearance of seasonal activity periods. As a result, populations’ activity periods and their synchronization became relevant aspects of ecosystems. This synchronization is based on historical correlation, therefore it is not maintained at individual timescales. Seasonal activity periods generate pre-possibilities, that is, combinatorial possibilities stemming from existing properties but 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 means e.g. in the specific case of the Kato & Miura (1996) network 40 over  $10^{655}$  — let us recall that physicists estimate that there are “only”  $10^{80}$  particles in the universe.

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, at least for the aspect we studied. However, such special configurations require an explanation. Here, the explanation is that ecosystems are a viable outcome of natural history. We do not mean that ecosystems are optimal, just that evolutionary history generates unlikely configurations at the ecosystem level by the evolution of their components (populations) by natural selection and the complexification of ecosystems over time (if



they do complexify). Being in this narrow domain is the condition of possibility for the complete ecosystem to exist and, thus, for the latter to maintain the entire state space in the model (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 consequences of the phenological change 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 can lead to a macrostate change. When this change corresponds to an entropy increase, it introduces randomness in the ecosystem with respect to viability. Specifically, the viability of the ecosystem’s populations defines this entropy and randomness for activity periods. In physics, such a definition is a theoretical step called coarse-graining, and this step is fundamental and irreducible because different coarse-graining may be chosen and it is required to define entropy (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 this is the case for the phenology changes resulting from climate change to a large extent. The notion of random change is critical since it addresses the fact that the change has no special property for viability, which is analyzed quantitatively with the Boltzmann schema. Figure 6B illustrates how the same level of randomness can be reached by a deterministic component and the random component of a Gaussian shift and that randomization, here, is not about the nature of the shifts. 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. Let us mention that our approach can be adapted to situations where a part of the change is random with respect to viability and another is not, primarily due to possible coevolution. Last, the core of our reasoning is the properties of the possibility space with respect to viability. If viability was a rather generic property, then disruptions in our sense could not occur for the aspect of interest. In other words, we assert that biological organizations have specific vulnerabilities due to their historical nature that lead them to be in specific configuration for some variables.

Analyzing anthropogenic disruptions in this framework led us to raise new questions. For example, we observed the effect of complete randomness for activity periods, i.e., maximum entropy, and found that, counter-intuitively, it 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 ecological networks for date and latitude. At the modeling level, disruption is analyzed, here, by modeling the situation before and after the disruption. Another path would be to use the dynamical systems framework, in which case the system would change attractor when the activity periods are the object of random perturbations.

Concerning theoretical principles, our approach opens new perspectives on articulating entropy and living systems. The entropy we describe is conceptually distinct from physics’s entropy because the latter has the physical dimension of energy per temperature. Moreover, we implement the notion that biological entropy should be defined with respect to biological organizations and, more generally, viability (Montévil, 2023; 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 appears in the notion of changing possibility space. The latter leads to a complementary quantity to entropy based on the entire possibility space’s size at a given time. This quantity is reminiscent of anti-entropy, a complementary quantity to entropy intended to describe biological complexity (Bailly & Longo, 2009; Longo & Montévil, 2012; Montévil, 2023). 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. When we consider a specific result of a history contributing to a system’s viability, disruption is the randomization of this specificity leading to a less viable situation. In other words, disruptions are direct or indirect consequences of specific causes that lead to loss of organization or impairment of the contribution of one or several parts of living systems to their ability to last over time, at a certain level of organization, via specific interactions that appeared over historical time. In the case we discussed, the viability of the complete ecosystem is limited to an extremely narrow part of the possibility space of activity periods, and this initial configuration is justified by evolution. Then, climate change leads to shifts that are random with respect to viability; thus, the system exits this viability zone, and, subsequently, many populations disappear. In other words, disruptions occur when the viability zone is a very small part of the possibilities, and a generic displacement will reduce the viability. As a result, we used and adapted the Boltzmann schema to address the structure of the possibility space with respect to viability. Since this schema is rather general, this approach can be transposed to other ecological phenomena.

As mentioned in the introduction, the concept of disruption is distinct from *perturbation* since it requires the reference to historical processes. In practice, it also implies that, when looking for possible disruptions, scientists should search for situations where viability, or functionality, is not a generic property of the system studied. Typically, the qualitative properties of the system are only met for a very small subset of the possible configurations, and the disruption acts by impacting the state of the system in this space. In this sense, it is also more specific than the concept of disturbance in ecology.

Disruptions are not about losing specific configurations coming from history *per se*; they are about situations where the loss of this specificity affects a system or an organization, thus, ultimately, viability. This perspective distinguishes the organizational perspective from the cybernetic one (Bich et al., 2020). Let us note that viability analysis includes everything in the model, including, in our case, robustness and agency, which are understood as components of plasticity and resilience. Thus, our analysis implies that, for this disruption, the specificity of the viable configuration remains when we account for the diverse plasticities and flexibilities of ecosystem relations.

Let us expand on this point. A disruption first randomizes a part of an organization or an ecosystem. In the model studied in this article, this process straightforwardly impacts viability, including robustness and resilience. We surmise that disruptions should impact variability, but the form of this impact can be diverse, in particular due to ecological plasticity. For example, flowering plants may not succeed in sexual reproduction due to the disruption of plant-pollinator interactions, but they may succeed in vegetative propagation. This case corresponds to what we have called elsewhere second-order disruptions, that is, disruptions that do not only impact a singular situation coming from history but the ability to generate functional novelties, here, by promoting genetic diversity (Montévil, 2023). Another typical situation is that disruptions would partly exhaust the redundancy in ecosystemic relations, making a system more vulnerable to future disturbances. A classification of the different situations by which disruptions can impact viability is beyond the scope of this paper but will be the object of future work.

A significant conclusion 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 the 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

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### 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

# A Models

In this appendix, we provide further details on the model.

## A.1 Overview of the model

The model has several main steps:

- The network comes from empirical data. The phenologies are generated as described in the section [A.2](#).
- The microstate change is generated according to the sampling method of interest, as described in section [A.4](#).
- We draw the consequence of this change according to the viability criteria described in section [A.3](#).

These operations are typically iterated when sampling the possibility space to determine the entropy of macrostates.

## A.2 Generation of phenologies

Initial networks stem directly from data; however, initial activity periods are unavailable. We designed a small algorithm to generate an initial configuration based on the statistics of a specific case. The relative complexity of the method stems from the fact that the real 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—nor viability conditions that we consider strictly at this step, that is without the possible robustness in the disruption analysis.

- Let us recall that we model populations directly which corresponds to the assumption that all individuals in a population start and end their activity simultaneously.
- 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 pollinator species, we choose the start of activity periods randomly between the earliest flowering among pollinated plants and the first pollinated plant finishing its flowering. Similarly, the stop of the activity period is chosen randomly between the first end and the last end of the flowering period among pollinated plants. Probabilities for these random choices are proportional to the logarithm of the available pollinated plants every day. This method is inspired by [Mommott 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, in which case the plant is removed.
- 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.3 Viability tests

**Plants** are viable when they are pollinated at least once: we neglect vegetative propagation or at least consider that sexual reproduction is necessary for survival.

**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  $a_0$  of looking for flowers (i.e., plants in their activity period) that they are not interacting with and that they could interact with because their activity period overlap. This parameter means that only some pollinator populations can forage on new plants, it is set to an arbitrary medium quantity 0.4. If the pollinator can establish new interactions according to the above test, then, for every day without a plant to pollinate and for every available plant, the pollinator has a chance  $a$  to establish an interaction, with  $a = 0.1$  in the article’s examples. Of course, this model is very simple; it can be complexified *ad libitum*, for example, using pollinators and flower morphology data to assess the possibility of such changes.

### A.4 Sampling of microscopic possibility space

To study disruption, we start with initial conditions obtained as described in section [A.2](#), we change activity periods as described below, and we assess viability as described in section [A.3](#).

#### A.4.1 Maximum entropy

To study maximum entropy configurations, for each population the start of the activity period is transformed randomly 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 population disappearances and, separately, the number of plant and pollinator disappearances.

Iterating this process leads to estimating the high entropy microstates’ frequency, as illustrated in figure [6A](#). 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.

Maximum entropy configurations are not very realistic, therefore we use another method in the next sections.

### A.4.2 Realistic entropy increase

For a realistic change in the starting time 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. \(2013a\)](#). Specifically, the latter are  $-1.58 \pm 16.3$  days for pollinators and  $-4.5 \pm 8.8$  for plants. Let us note that a negative shift means a earlier activity and that the times of year are considered modulo 365. 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 6B, we use 200 samples on every point of a  $150 \times 150$  grid.

### A.4.3 Systematic exploration of possibility space

**Estimation of  $\log(\omega_d^a)$**  For  $n$  species (plants and pollinators), with for each species the starting day of activity being a whole number within the range from 1 to 365, the number of possibilities of their starting days 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  $\|\cdot\|_\infty$  (i.e., balls that are boxes) of increasing radius  $\rho_k = k$  days (for increasing  $k$  from 0 to 182) centered on the initial conditions  $x_i^i$ ,  $B_{\rho_k}(x_i)$ . We also sample balls centered on  $\bar{x}_i^i$ , 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  $(2\rho_k + 1)^n$ , and we ensure that the ratio between the volume of two successive balls is larger than the sampling rate to minimize overlaps by excluded  $k$  when the the ratio between the volume for  $k$  and  $k - 1$  is smaller than the sampling number. Then,

$$\widetilde{\omega}_d^i = \sum_k N_{\rho_k, d, N} \frac{(2\rho_k + 1)^n}{N}$$

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

This method has a drawback : for macrostates with low entropy, it will only detect the contributions around the initial condition – the contributions of other parts of the possibility space are too rare to be obtained randomly. However, they do exist. Let us consider, for example, the disappearance of a pollinator that interacts with a single plant (the latter being also otherwise pollinated). All activity periods of the pollinator that do not overlap with the plant’s activity period lead to the same macrostate. As a result, we include a heuristic correction term:  $\widetilde{\omega}_d^{n-1/n} + \log(365)^{1/n}$  for a disappearing pollinator with only one interaction (we consider that most starting times would lead to its extinction). More generally, we use:  $r(d) = \sum_{i=1}^d 1/k(i)$ , where  $k(i)$  is the number of interactions of the pollinator  $i$  (sorted by increasing number of interactions).

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

This correction is heuristic and only significant for pollinators with one or two interactions, that is, for low values of  $k(i)$ .

**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  $m$  ( $m = 10$  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 ecological network changes due to disappearances and possibly agency, so each evaluation is done with the corresponding network.

To estimate  $\log(\omega_0^f)$  for a given microstate, we use the changed network described above and the initial microstate and follow a similar scheme to estimate  $\log(\omega_d^i)$ . The main difference is that we perform a binary search for the largest ball where all populations survive instead of sampling every ball. In the paper’s simulation, we take 20 samples per ball and iterate the estimation 400 times.

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