On-off intermittency and irruptions in host-parasitoid dynamics

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ABSTRACT

Environmental stochasticity affects population dynamics in a variety of ways, including the possibility of drastic modifications in the stability properties of the ecosystem. In this work, we investigate a case of coupled host-parasitoid dynamics adopting Beddington's conceptual two-dimensional map. We stochastically perturb some of the parameters controlling either the host dynamics or the host-parasitoid interaction, observing a dramatic change in the system dynamics with the emergence of on-off intermittency, a behavior characterized by the irregular alternation between quiescent phases and sudden population bursts. This phenomenon is herein offered as a qualitative, environmental-based description of population outbreaks.

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1. Introduction

Population fluctuations are a core component of ecological dynamics, and can be generated by internal feedback processes and/or by external environmental drivers, often mimicked by environmental stochasticity (Turchin, 2003). Sudden population outbreaks in host-parasitoid systems, also called irruptions, are a paroxysmic form of population fluctuations which stand out as an intriguing and practically relevant topic (Hassell, 2000). Pest outbreaks, in particular, have received much attention owing to their ecological and economic relevance (Barbosa et al., 2012).

Parasitoid outbreaks did not receive the same amount of attention as sudden pest growths (Ludwig et al., 1978), even though the phenomenon has been discussed in the literature (Ford and Ford, 1930; Hill and Caswell, 2001; Ehrlich and Hanski, 2004). The relevance of weather conditions has been studied in the case of aphids (Weisser et al., 1997), finding that searching rate (quantified by the visited number of aphid colonies and rose bushes) and growth rate (in terms of the reproductive success of foraging females) are considerably affected by adverse meteorological conditions such as wind and rain.

In past years, the impact of environmental stochasticity on population outbreaks was studied in various models. In a host-pathogen-predator model (Dwyer et al., 2004), irregular outbreaks were interpreted as an outcome of the weather-forced interaction between a stable point associated with the predator action and limit cycles induced by the pathogen, thus focusing on the interaction between multiple species. Another approach considered a prey-predator model in which the species were coupled through a type III functional response (Spencer and Collie, 1996). In such model, the predator equation was stochastically forced by red noise, leading to irregular fluctuations between high and low prey equilibria and causing the insurgence of outbreaks in both species. In a model composed of two competing preys and one predator active only during summer (Hanski and Henttone, 1996), environmental stochasticity was included by linearly varying the number of predators at the beginning of each summer.

In this paper we focus on the coupled dynamics of a host-parasitoid system and further explore the role of environmental forcing in generating outbreaks. Model-wise, one of the earliest approaches was proposed by Nicholson and Bailey (1935), who introduced a two-dimensional map reproducing the host-parasitoid dynamics. This approach, however, showed a problematic flaw, resulting in unstable oscillations in the size of the populations. Later, Beddington (1975) introduced an exponential density-dependent self-regulation (already considered by May (1974)) as a stabilizing factor in Nicholson-Bailey's model, thus providing a reliable—yet simple—way to describe the interaction between the population of the parasitoid and that of the parasited host.

A two-dimensional model—such as Beddington's—is a crude representation of the desired dynamics, and it does not include complicating but crucial ecological phenomena such as climate and environmental variability, that can have remarkable effects on the system dynamics. Conditions such as drought and severe weather can affect the species growth rate or their ability to find resources, for example, and those can in turn affect the size of

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the populations. One simple way to represent these effects is to introduce a stochastic perturbation in some of the main model parameters, leading to random variations in the strength of species interactions. As we show here, such parametric perturbation can lead to the occurrence of on-off intermittency, a feature that could qualitatively describe abrupt changes in the population size (Ehrlich and Hanski, 2004; Schowalter, 2016).

In dynamical systems, *intermittency* is the term used to describe the switching behavior between different regimes. Initially observed in turbulence (Batchelor and Townsend, 1949), the phenomenon rapidly caught the attention of the scientific community, which categorized it in a few different typologies. Here we focus on the case of *on-off intermittency* (Platt et al., 1993), which describes the alternation between quiescent phases (often called also *laminar phases*, mainly in physics-related disciplines) and sudden bursts of activity generated by the temporally-varying stability of an invariant set (in the simplest case, a fixed point) as determined by the value of an external control parameter.

Several systems showed on-off intermittency, ranging from the solar cycle (Platt et al., 1993) and earthquakes (Bottiglieri and Godano, 2007) to electronic circuits (Hammer et al., 1994) and the electrodynamics of liquid crystals (John et al., 1999). Most theoretical aspects of the phenomenon were studied when focusing on simple population dynamics models, usually employing the logistic equation (Platt et al., 1993; Heagy et al., 1994; Toniolo et al., 2002; Metta et al., 2010; Moon, 2010); proofs of its occurrence in even slightly more complex dynamics, which e.g. aim to describe the behavior of a few trophic levels, are still rare (Vissio and Provenzale, 2021).

To study outbreaks in the Beddington host-parasitoid model, we first allow the host grazing intensity to be affected by random forcing, showing the occurrence of on-off intermittency in the host dynamics. We then apply stochastic forcing to the parameters related to parasitoid activity, either the searching efficiency or the growth rate. The properties of the perturbed systems are qualitatively compared with the unperturbed case to gain insight in the role of environmental stochasticity. Finally, we investigate the dynamics of on-off intermittency when coupled maps are considered, i.e. when we take into account that different sites could exchange some individuals.

Section 2 describes the properties of on-off intermittency, outlining results from previous studies that motivated this work. Section 3 introduces Beddington's model, describing the procedure used to introduce stochastic forcing and the details of the numerical integration. In Sections 4,5,6 we illustrate the behavior generated by environmental stochasticity and the conditions for which on-off intermittency is generated. Section 7 summarizes our results and outlines possible developments.

2. On-off intermittency

A system is defined *intermittent* when its dynamics shows an irregular alternation between different states. In the case of *on-off intermittency*, the system undergoes irregular transitions between *quiescent* or *off* phases—whose duration follows an approximate power law distribution, at least in the simplest cases—and abrupt activity *bursts* or *on* phases.

In this kind of intermittency, quiescent phases are due to the existence of an invariant manifold (e.g. a fixed point), which is attractive enough to allow for long, stable phases during which the system lingers in the vicinity of the temporally stable attractor. Remaining near this manifold for relatively long times, the system displays the quiescent phases. Suddenly, however, the volatility of an external parameter controlling the stability causes the manifold to become unstable and the system to burst away.

In the simplest cases, the phase-space location of the invariant manifold is independent of the external control parameter, which determines only the manifold stability. Also, the fluctuations of the external parameter are usually taken to be independent of the system state (i.e., it is a driven system where the driver is independent of the driven component, that is a skew-product configuration).

Owing to the potential role of this concept to qualitatively describe bursting behavior, in past years on-off intermittency has received some attention by the scientific community.

Platt et al. (1993) and Heagy et al. (1994) enlightened the fundamentals of the phenomenon, the latter deriving the power-law underlying the distribution of the duration of quiescent phases for maps with the specific form $y_{n+1} = z_n f(y_n)$ (with the variable z_n taken from a random or a chaotic process). Later on, Toniolo et al. (2002) inspected the occurrence of on-off intermittency in a stochastically driven logistic map. In their papers, Metta et al. (2010) and Moon (2010) examined Toniolo's framework in the context of coupled logistic equations, the former focusing on kurtosis as an index to identify on-off intermittency, the latter putting the spotlight on intermittency in coupled systems, an approach of particular interest for the study presented here (see Section 6).

In past years, several works explored the emergence of intermittent dynamics in population models. Using a double map simulating competing species and applying stochastic driving to the whole system, Ferriere and Cazelles (1999) found the quiescent-phase power law $D^{-\frac{3}{2}}$. Interestingly, De Feo and Ferriere (2000) found on-off intermittency using the same model without random forcing, although a close inspection of the time series shows that the outbursts are not as abrupt as in the stochastic case, rather resembling randomly increasing fluctuations with a wave-like structure. While Ferriere and Cazelles (1999) used multiplicative noise, Sharma et al. (2015) used additive random noise to force the Ludwig model Ludwig et al. (1978). Considering both white and, more markedly, red noise, these authors found that the temporal dynamics of the spruce budworm population clearly appears similar to on-off intermittency. Finally, Vissio and Provenzale (2021) extended the study of on-off intermittency in population dynamics to stochastically forced systems of ordinary differential equations in a three-species food chain.

3. Host-parasitoid model

The dynamics of host and parasitoid populations can be modelled by the two-dimensional map introduced by Beddington (1975), Kot (2001), and Edelstein-Keshet (2005) as an extension of the Nicholson-Bailey (NB) model (Nicholson and Bailey, 1935). Since the original NB model predicts unstable oscillations for both populations, Beddington implemented a stabilizing factor, expressing the host reproductive rate as the exponential of the logistic increment (Moran, 1950; Ricker, 1954; May and Oster, 1976), $\exp\left[r(1 - \frac{N}{K})\right]$. Thus, the model equations become:

$$N_{t+1} = \delta N_t \exp\left[r\left(1 - \frac{N_t}{K}\right) - aP_t\right], \tag{1}$$

$$P_{t+1} = bN_t[1 - \exp(-aP_t)], \tag{2}$$

where N and P represent the biomass of, respectively, the host and parasitoid components, while r and K are respectively the growth rate and the carrying capacity of the host. The parameter δ, when constant, can be rescaled and in the original Beddington model was thus fixed as $\delta = 1$. Finally, a and b are, respectively, the searching efficiency and the growth rate (with respect to the host population) of the parasitoid. Neglecting the parasitoid presence, thus setting $P = 0$, reduces the system to the classic Moran-Ricker model

(Moran, 1950; Ricker, 1954). Depending on the values of the parameters, the Beddington model can exhibit different regimes from stable fixed points to chaotic dynamics. Here, we show that including stochastic variability in the parasitoid searching efficiency or growth rate leads to the occurrence of alternating quiescent phases and bursts—i.e. to on-off intermittency.

In the original (deterministic) version of the model, all parameters were constant. Here, some of them are allowed to vary stochastically, that is we take either

$$\delta = \Delta\epsilon \tag{3}$$

for the case of environmental stochasticity acting on the host, and either

$$a = A\epsilon \tag{4}$$

or

$$b = B\epsilon \tag{5}$$

for the case of environmental stochasticity acting on the parasitoid. Here, Δ, A and B are constant maximum values and ϵ is a random number uniformly distributed between 0 and 1.

Throughout the paper we consider three different versions of the model, one with fixed values of the parameters and the others with either δ, a or b allowed to vary stochastically as described above. The chosen values for the parameters are:

- Fully deterministic: $\delta = 1$, $a = 0.7$, $b = 0.7$
- Stochastic variability of δ : $\Delta = 0.15$, $a = 0.7$, $b = 0.7$
- Stochastic variability of a : $\delta = 1$, $A = 0.6$, $b = 1$
- Stochastic variability of b : $\delta = 1$, $a = 1$, $B = 0.6$

We recall that, in the above list, lower case letters represent fixed parameters, while upper case letters are the coefficient of the random number ϵ. See Appendix A for details on the choice of the parameters for the stochastic a and b cases—stochasticity in the host parameter is addressed in a qualitatively similar methodology. In all settings we use $r = 3$ and $K = 10$, with initial conditions $N = 10$, $P = 5$. Each run has spin-up and run times of, respectively, 10^5 and 10^7 time steps.

In the fully deterministic setting, the system displays chaotic dynamics; Fig. 1 (left panel) shows a typical parasitoid time series for this case.

Following Toniolo et al. (2002), in what follows we define as off-phase those continuous time intervals during which the parasitoid biomass P_n (or, in Section 4, the host N_n) is below a specific threshold, here chosen as 0.001 (other choices lead to analogous results). Such "off-phases" are not explicitly definable in the deterministic, non-intermittent case.
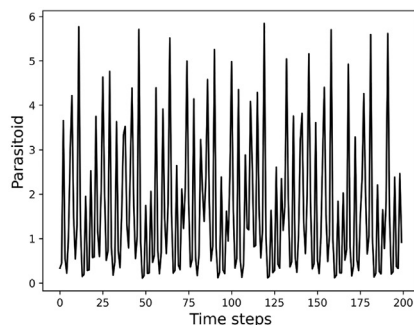
Fig. 1 (right panel) shows the parasitoid time series for the Stochastic b case—the Stochastic a case is qualitatively similar. The alternation of on and off phases distinctly stands out, with the former suddenly interrupting the latter with no apparent regularity.

We must point out that, when employing stochastic parasitoid parameters, after a large number of iterations the parasitoid populations can get extinct, reaching the *zero* stable state. Checking this behaviour with different numbers of digits to represent the variables indicates that it depends on the numerical approximation—i.e., the collapse to zero happens on longer times for higher precision and it would not happen if we could achieve infinite precision. In order to practically overcome this behavior, when a parasitoid population cancels out we force it to assume a value $10^{-12}\epsilon$, with ϵ a random number uniformly distributed between 0 and 1. This could also be taken as a representation of a (very small) immigration of individuals from a regional pool or of the existence of a small refugium. Another way to address this problem is to add a very small term $10^{-12}\epsilon$, where ϵ is a random number uniformly distributed between 0 and 1, to the right side hand of Eq. 2 therefore directly including a small random immigration term. The two approaches provide equivalent results and in the following we adopt the first strategy. A detailed discussion of the results obtained using the random immigration term is given in the Supplementary Information, where we also explore an alternative stochastic perturbation of the model parameters, confirming the results reported below.

Following the approach proposed by Moon (2010), we also inspect locally connected maps, coupling them with the structure:

$$N_{t+1}^k = (1-\gamma)f_N(N_t^k; a_t^k) + \frac{\gamma}{2}\left[f_N(N_t^{k-1}; a_t^{k-1}) + f_N(N_t^{k+1}; a_t^{k+1})\right], \tag{6}$$

$$P_{t+1}^k = (1-\gamma)f_P(P_t^k; a_t^k) + \frac{\gamma}{2}\left[f_P(P_t^{k-1}; a_t^{k-1}) + f_P(P_t^{k+1}; a_t^{k+1})\right], \tag{7}$$

where f_N and f_P are defined by the right hand side of Eqs. 1,2 and the superscript k defines a specific location, with $k-1$ and $k+1$ representing the neighboring maps coupled to this location.

4. Intermittency in host dynamics

Bursting behaviour in host populations can have dramatic impacts on ecosystem functions and services. On-off intermittency in host dynamics can emerge in Beddington's model by including stochastic variations in the intensity of grazing by the host, suitably modelled by allowing the pre-factor δ in Eq. 1 to become variable in time. Adopting $\delta = \Delta\epsilon$ with $\Delta = 0.15$ (where ϵ is a random number uniformly distributed between 0 and 1) leads to on-off intermittency for the host dynamics.
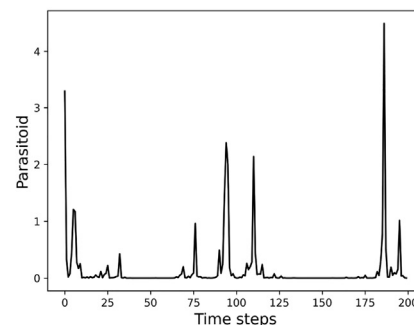

Fig. 1. Left: chaotic parasitoid dynamics in the Beddington model for the fully deterministic case. Right: intermittent parasitoid dynamics in the Beddington model for stochastic variations of the b parameter.

Heagy et al. (1994) and Toniolo et al. (2002) showed that a power-law distribution of quiescent phases is a distinctive feature of on-off intermittency. In such works, the probability of having a quiescent phase lasting D steps was shown to be proportional to $D^{-\frac{3}{2}}$, at least for the case $y_{n+1} = z_n f(y_n)$, as mentioned in Section 2. A much steeper dependence was instead found for the non-intermittent dynamics of the same models.

Fig. 2 shows a time series of the host population and the probability distribution of the quiescent phase duration D for this case. The quiescent phase duration approximately follows the power law $D^{-\frac{3}{2}}$, in keeping with the occurrence of on-off intermittency. Larger values of Δ, on the other hand, did not generate host population intermittency.

For a random variability of the grazing intensity we have always observed the extinction of the parasitoid, when the host dynamics is on-off intermittent. For larger values of Δ—starting at $\Delta = 0.2$—the host undergoes non-intermittent chaotic dynamics and the parasitoid survives, developing a dynamics similar to on-off intermittency but with longer quiescent phases. The extinction of the parasitoid when host intermittency is present is explained by the fact that during the quiescent phases the host biomass stays at values that are too small to support a permanent parasitoid population. A different situation is encountered in the case of a metapopulation of hosts distributed in nearby sites, controlled by a single parasitoid population able to attack the most abundant site, as discussed in Section 6.

5. Bursting parasitoid dynamics

In this Section we discuss the effects of stochastic perturbations on some of the parameters related to the parasitoid activity in Beddington's model—corresponding to the "Stochastic a" and "Stochastic b" cases.

The stochastic driving here inserted in Beddington's model—as discussed in Section 3—modifies one of the parasitoid-related parameters, leading to modifications in the overall dynamics. As a first step in the analysis, we inspect how these changes impact the evolution of the whole system, checking the possible values reached by the host and the parasitoid given the state of the parasitoid at the previous time step. That is, we look at the region of phase space spanned by the system.

Fig. 3 (left panel) shows P_{n+1} versus P_n. The area spanned by Stochastic a case is, by far, the largest of the three cases considered. On the contrary, in the Stochastic b case the range of values covered by the parasitoid is smaller than in the purely deterministic case. Fig. 3 (right panel) shows N_{n+1} versus P_n. The differences between the models are astounding: whilst in deterministic case a high value for P_n inevitably corresponds to a low value for N_{n+1}—and this behaviour is even more emphasized in Stochastic b case —, the application of the random driving for the searching efficiency leads to a much more complex dynamics where N_{n+1} spans a large set of values even for large P_n.

From Fig. 3 we infer that environmental-induced changes in the searching efficiency affect the host-parasitoid dynamics in a much stronger way than in the case of a variable parasitoid growth rate. Indeed, the same stochastic formulation—with the same coefficient—applied to the two parameters leads to different results. In particular, whilst a high value of P_n generally leads to a comparatively lower value of P_{n+1}, a random searching efficiency does not lead to the same behavior for the future state of the host.

As shown in Fig. 4, the probability distribution of the parasitoid quiescent phase duration, D, in the intermittent cases follows an approximate power law at least for moderate values of D. For comparison, the classic reference slope $D^{-\frac{3}{2}}$ is also reported; the power law detected in the model adopted here is slightly steeper than $-3/2$, indicating that longer quiescent phases are slightly less likely to happen. A possible explanation of the difference between Beddington's model results and the logistic equation relies on the higher complexity of the former, whose equations are asymmetrical and represent two populations evolving with different dynamics. This difference stands out even when comparing the case of host intermittency—we recall that just the host is active, due to parasitoid extinction—in Fig. 2 with parasitoid intermittency in Fig. 4.

The power spectrum is another useful statistics to characterize the properties of on-off intermittency in discrete-time dynamical systems. In many (simple) cases, non-intermittent discrete-time chaotic dynamics is characterized by white or blue spectra (i.e., spectra that are either flat or grow at high frequency, respectively) (Cohen, 1995). In the on-off intermittent case, by contrast, the presence of strong spikes leads to the prevalence of "red" spectra, where the spectral energy is larger at lower frequencies (Balmforth et al., 1999). In general, however, the situation could be more complicated and a red spectrum cannot always be taken as a proof of the presence of intermittency (Reuman et al., 2006).

The power spectra of the parasitoid for the three cases considered are shown in Fig. 5 (left panel). Both stochastically-perturbed settings clearly show a "red" power spectrum in most of the domain, especially at low frequencies. Instead, the deterministic setting displays, as expected, a "blue" character, with dominance of energy at high frequency.

The inspection of the power spectra of the host in Fig. 5 (right panel) reveals that the two stochastic settings show a nearly identical behavior, at least for the parameter choices adopted here. In general, the specific form of the spectra depends on the range of stochastic variations of the a and b parameters, but lead to "red" spectra at low frequency anyway.
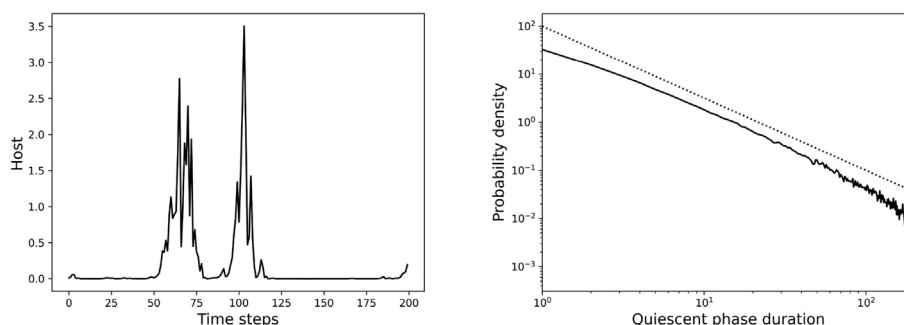

Fig. 2. Left: a time series of the host population for a case in which the host undergoes on-off intermittency. Right: probability distribution of the quiescent phases in the host time series. Dotted line: $D^{-3/2}$.
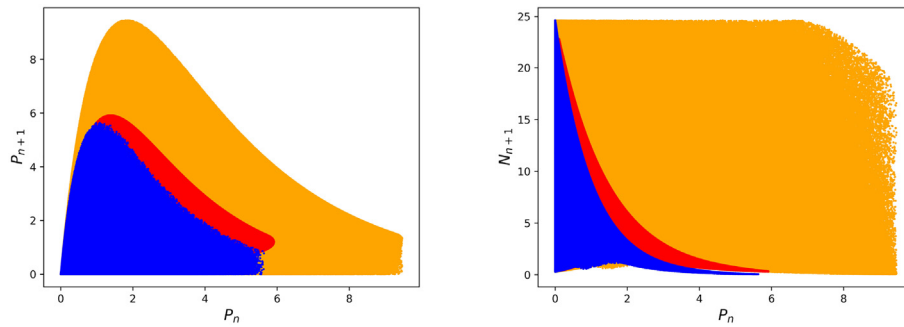
Fig. 3. Red (medium gray in b/w), Deterministic. Orange (light gray in b/w), Stochastic *a*. Blue (dark gray in b/w), Stochastic *b*. (left panel) P_{n+1} versus P_n; (right panel) N_{n+1} versus P_n.
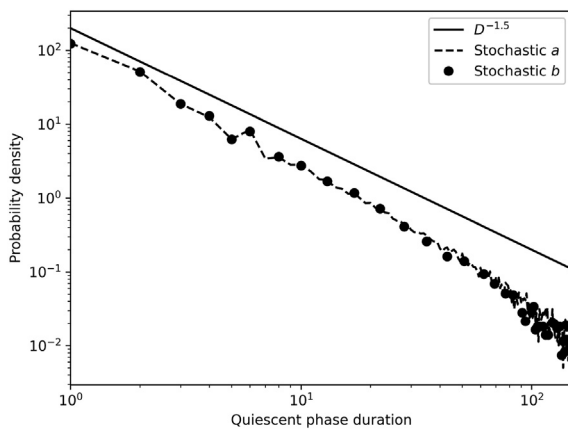

Fig. 4. Probability distribution of the quiescent phases.

6. Locally coupled maps

We now turn to a preliminary investigation of the dynamics of a chain of locally coupled maps, as described by Eqs. 6,7. We consider a set of 10^2 coupled maps with periodic boundary conditions at the two ends of the chain. Spin-ups and runs are set to, respectively, 10^5 and 10^6 time steps.

6.1. Host intermittency

Using Eq. 6 to represent the coupling between different sites, we build a metapopulation of 100 coupled maps for the host with only a single parasitoid population to predate it. Supposing that the latter can instantaneously reach the node with the largest host biomass, it is possible for the host to undergo on-off intermittency and

for the parasitoid to survive in time—typically with chaotic dynamics.

Fig. 6 shows such a case: here the Stochastic δ scenario, with different nodes coupled with $\gamma = 0.001$, provides different host populations interacting with each other through mutual exchange of individuals. The single parasitoid population is able to move rapidly to the site where the host is more abundant. This strategy allows the parasitoid to survive, in spite of the average host biomass being too low to assure parasitoid permanence.

6.2. Parasitoid intermittency

We then turn to parasitoid intermittency and stochastically force the searching efficiency *a*. First, we consider the case $a = A\epsilon$ with $A = 0.6$, that is the stochastic *a* case of previous sections (hereafter we always consider the case $r = 3$, $b = 1$). Decoupling the maps—i.e. setting $\gamma = 0$ in Eq. 6–7—leads to independent on-off intermittent behavior for each map as already discussed above. An Hovmöller diagram—Fig. 7 (left panel)—shows the scarcity of peaks in the time series of the maps, whose identification number is reported on the horizontal axis. Time runs vertically from bottom to top. The probability density of the quiescent phase duration is the same as in Fig. 4. Increasing γ to a very small value completely modifies this behaviour, leading to much more frequent peaks with respect to the previous case and to the disappearance of the power-law distribution of quiescent phases for the individual maps. Fig. 7 (right panel) shows the Hovmöller diagram for the case $\gamma = 0.0001$.

An interesting behavior appears when we set $A = 0.4$. For the uncoupled case, this value of A leads to the extinction of the parasitoid. Instead, a coupling strength $\gamma = 0.005$ leads to the appearance of on-off intermittency, see Fig. 8 (left panel). That is, allowing the species to be exchanged across adjacent sites is enough to prevent them from extinction and to generate sudden bursts in population size. Interestingly, this indicates the possibil-
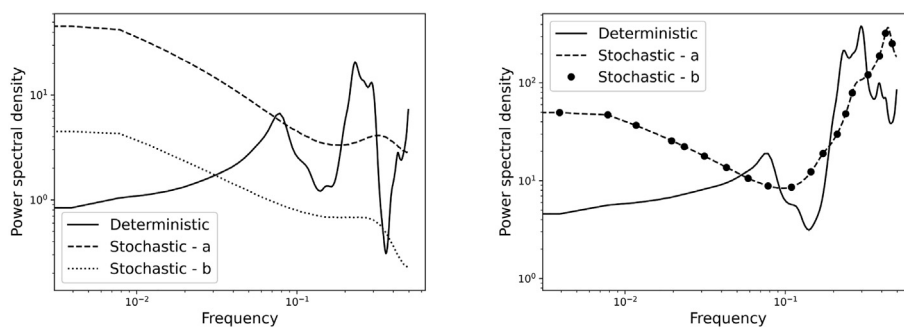

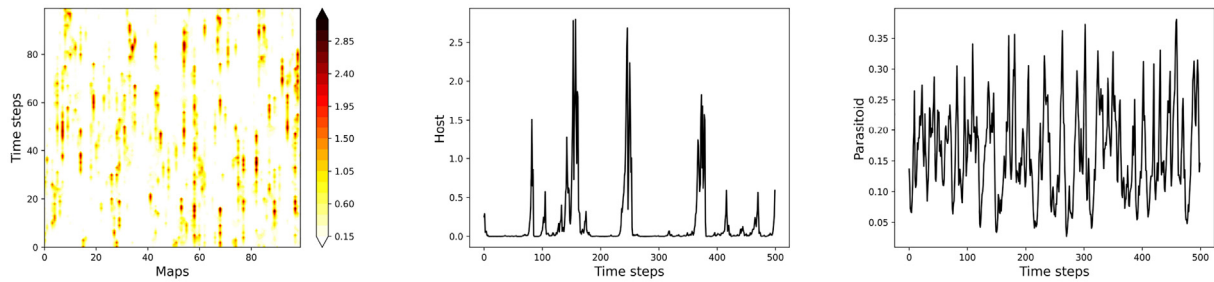**Fig. 5.** (left panel) Power spectra of the parasitoid; (right panel) Power spectra of the host.

Fig. 6. Case with host coupled on multi-dimensional map and single map parasitoid. Left: Hovmöller diagram of the host. Center: Host time series in one node. Right: Parasitoid time series.
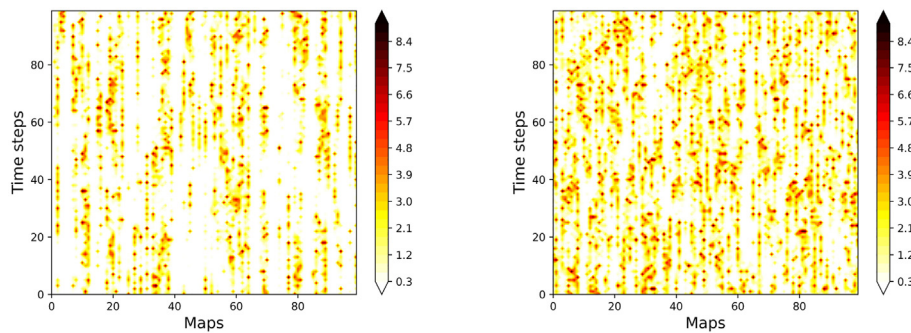

Fig. 7. (left panel) Hovmöller diagram for $\gamma = 0$; (right panel) Hovmöller diagram for $\gamma = 0.0001$. Stochastic a case, $0 \leqslant a \leqslant 0.6$.
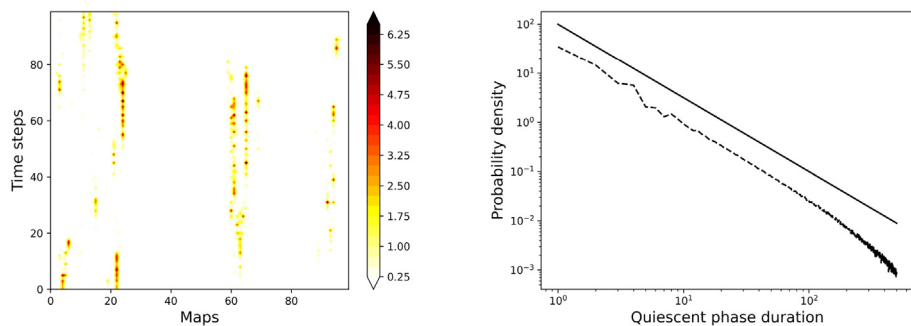

Fig. 8. Stochastic a case, $0 \leqslant a \leqslant 0.4$, $\gamma = 0.005$. Left panel: Hovmöller diagram. Right panel: probability distribution of the quiescent phase duration.

ity of population outbreaks in coupled spatial-temporal dynamics for parameter values that would lead to extinction in isolated populations. On the other hand, a significant increase in the coupling strength (e.g., employing $\gamma = 0.05$) leads to fully chaotic dynamics. It is worth to mention that spatially induced chaos has already been shown in population dynamics models (Pascual, 1993).

The probability distribution of the quiescent phase duration for each individual map closely follows a power law $D^{-\frac{3}{2}}$, as shown in Fig. 8 (right panel) and it is consistent with the results of Heagy et al. (1994), Toniolo et al. (2002), Metta et al. (2010), Moon (2010), and Vissio and Provenzale (2021). In this coupled system, longer quiescent phases appear to be more likely to occur than for the case of individual uncoupled maps shown above, generating on-off intermittent behavior with the well-known distribution of quiescent phases.

The outcome of this preliminary exploration of coupled maps is that spatial coupling, inserted through local interactions of the populations, can significantly affect the dynamics with unexpected outcomes, e.g. inducing or suppressing on-off intermittency when the same uncoupled systems would respectively become extinct or undergo on-off intermittency.

7. Discussion and conclusions

We have discussed the effects of stochastic variations in the control parameters of a host-parasitoid model system, to simulate the impact of environmental variability. We have shown that, under suitable conditions, the parameter fluctuations induce the onset of on-off intermittency, in which chaotic bursts suddenly interrupt quiescent phases whose duration has an approximate power-law distribution. Analogously, the analysis of the parasitoid power spectra has indicated that the stochastically-driven host-parasitoid systems display red spectra.

Beddington's model is a solid—albeit simple—testbed to study intermittent outbreaks in more than a single trophic level, i.e., for more than an individual component such as in the case of the logistic map considered in past works.

We have started introducing stochastic variability in the intensity of grazing in Eq. 1 showing that, for the stochastic forcing chosen, it leads to the emergence of on-off intermittency for the host dynamics, giving a qualitative, environmental-based explanation for, e.g., pest irruptions, a case of particular relevance for practical purposes. In such cases, however, Beddington's model always pre-
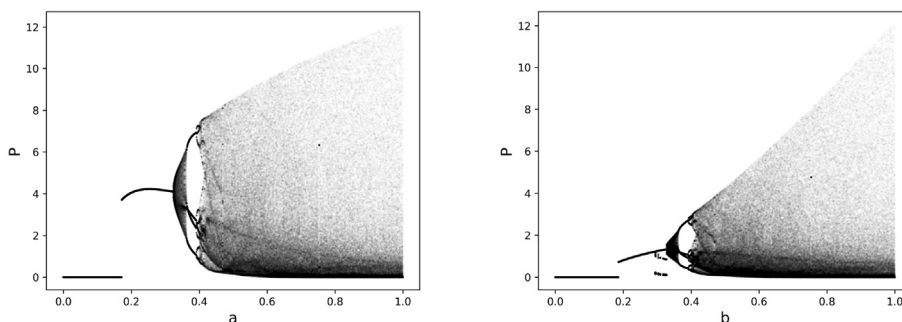
Fig. A.9. Orbit diagrams depicting parasitoid attractors in Beddington's model. (left panel) $b = 1$, $r = 3$, P vs a; (right panel) $a = 1$, $r = 3$, P vs b.

dicted the extinction of the parasitoid population, except when a single parasitoid population is allowed to predate the momentarily largest host population in an ensemble of spatially coupled sites. In this case, of relevant practical interest, the host population fluctuated intermittently in time and space while the parasitoid population survived and controlled it.

When environmental stochasticity affects the parasitoid vital rates and control parameters, we observed that the range of values spanned by the parasitoid population dramatically increased. In this case, the parasitoid population size at a given time influences the subsequent state of both the host and parasitoid populations in different ways that depend on which of the three settings is considered.

We have also shown that adding local coupling to a set of individual host-parasitoid systems can have relevant effects, such as hamper the presence of intermittency in cases when the uncoupled individual systems were intermittent or, conversely, generate on-off intermittency for populations that in isolation were otherwise bound to go extinct.

Throughout the paper we have simulated the effect of environmental variability in terms of stochasticity in the parameter values. Indeed, this kind of approach provides a reason—which plunge its roots in, e.g., weather conditions—for the occurrence of irruptions in natural populations. Further developments of this approach could for example consider a case with bistability between a strictly nonzero fixed point and a cyclic or chaotic attractor, or between two chaotic states. Particularly relevant will be the further exploration of the consequences of hierarchical and/or spatial coupling (Balmforth et al., 1999; Balmforth et al., 2002). In any case, the processes analyzed here qualitatively describe the occurrence of population outbreaks, where the quiescence of a given population is abruptly interrupted by irregular and violent increases in its size.

Code Availability

Code used in numerical simulation can be found at https://figshare.com/articles/software/On-off_intermittency_and_irruptions_in_host-parasitoid_dynamics/16744048 (last accessed on 30 March 2022).

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CRediT authorship contribution statement

Gabriele Vissio: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Antonello Provenzale:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Bifurcations

As many other models, Beddington's map dynamics changes with respect to the values chosen for the parameters, switching from stability to multistability and to (eventually) chaos following different routes (Xu and Boyce, 2005). A useful method to show this is employing orbit diagrams (Ott, 1993; Thompson and Stewart, 2002; Strogatz, 2014), where the projection of the system's attractors on one dimension is plotted with respect to a specific parameter. This is important for our approach since, e.g., for specific values of the parameters b and r, we need to replace a with a stochastic factor suitable to drive it in and out the chaotic dynamics range, without lingering excessively into it. This case is depicted in Fig. A.9 (left panel), where we can see that, for $b = 1$ and $r = 3$, $a = 0.7\epsilon$ is a reasonable choice to reproduce the desired behaviour. We remind that ϵ represents a random number picked from a distribution uniformly distributed between 0 and 1. Fig. A.9 (right panel) shows the orbit diagram of the system attractor as a function of b for $a = 1$ and $r = 3$. Again, $b = 0.7\epsilon$ is a convenient choice for the stochastic parameter.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.jtbi.2022.111174.

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