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Review

Stable epidemic control in crops based on evolutionary principles: Adjusting the metapopulation concept to agro-ecosystems

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ABSTRACT

In agro-ecosystems, epidemics reduce crop yield. Disease development depends on interactions in time and space between host plants, pathogens, the environment and humans. There is an urgent need to reconsider disease control tactics by linking ecological and evolutionary concepts at the landscape scale, as achieved for natural ecosystems. The aim of our work is to adjust the geographic mosaic of coevolution theory between hosts and pathogens to agro-ecosystems. In agro-ecosystems, adaptation dynamics at the landscape scale depend jointly on annual epidemics, the flow between demes, and human actions, which exacerbate homogeneities in time and space. We describe a framework to take into account these direct and indirect human actions on host agro-metapopulations, which influence the size and composition of pathogen agro-metapopulation demes. By linking disciplinary concepts it becomes possible to optimize the stabilization of disease control efficacy by designing management strategies to selectively apply evolutionary costs. At present, the pathogen agro-metapopulation adapts to its host and the other way around does not occur. However, these evolutionary costs can be used to maintain the pathogen agro-metapopulation locally non-adapted to the host agro-metapopulation. The use of this framework will allow crop protection approaches to be redesigned by modifying the host agro-metapopulation dynamics depending on the observed state of the pathogen agro-metapopulation.

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1. Introduction

In agro-ecosystems, human activity determines plant population dynamics and therefore has an impact on the development of disease epidemics. An ecosystem is defined as “a dynamic complex of plant, animal, and microorganism communities and their non-living environment interacting as a functional unit” (Millenium Ecosystem Assessment, 2005). Thus in the broadest sense an “agro-ecosystem” includes all managed and unmanaged environments, domesticated and wild communities as well as human communities (Loucks, 1977). In natural ecosystems, plant lifecycles determine their population dynamics in space and time (Gilbert, 2002). In turn, pathogen lifecycles evolve to exploit resources from host plants, which are related to the environment (Agrios, 2005). In contrast, in agro-ecosystems, plant population dynamics are also controlled by anthropogenic choices, because plant populations are organized into crops and managed toward production goals. In these crops, epidemic development depends on the interaction in time and space between host plants, pathogens, the environment and humans (Agrios, 2005). Major changes associated with

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agricultural intensification (Stoate et al., 2009) and pesticide availability made it possible to control biotic competition by weeds, pests and pathogens, and thus grow monocultures on large acreages. This had the unintentional effect of increasing the vulnerability of crops to diseases (Stukenbrock and McDonald, 2008). In this paper, we mainly focus on adaptation of a fungal pathogen to plant resistance. However, the theories discussed could be extended to other pathogens such as bacteria, viruses or insects, and to other control tactics such as fungicide use or cropping practices. Major changes associated with agricultural intensification also increased the dependence of production systems on pesticides, the usage of which we now wish to reduce.

As epidemics reduce crop yield, strategies combining several tactics are deployed to control them. Crop protection management strategies have the dual aim of achieving efficient and stable epidemic control. Their efficiency – i.e. capacity to produce an effect at one point of time and space – depends on pathogen biology and population size (Bousset and Chèvre, 2012). Their stability – i.e. the persistence of their efficacy in time and space – depends on adaptation dynamics in pathogen populations (Brun et al., 2010). In recent decades, concerted efforts have been dedicated to increasing efficiency; however maximizing efficiency failed to provide stability (Stukenbrock and McDonald, 2008). For example, the deployment of a limited number of resistant host varieties leads to an increase of compatible individuals in pathogen populations (Brown and Hovmøller, 2002). This in turn causes a loss of efficiency and "boom and bust" cycles over time (Browning and Frey, 1969). The underlying cause for this variation in efficiency is a change in the average level of adaptation of the pathogen population to the control tactic (Brun et al., 2010; Rouxel et al., 2001). The pathogen continuously adapts to the mosaic of host fields occurring at the landscape scale. Nevertheless, today the deployment (characteristics and localization) of each crop at the landscape scale is not chosen by taking into account the average level of compatibility of the pathogens present. Thus, there is room for improvement, to at least adjust the host in real time, or even to strategically anticipate changes in the pathogen population. Despite the need to consider evolutionary principles in crop disease management strategies, links between agronomic disciplines and evolutionary studies (Chevassus-au-Louis, 2006) are still lacking

To challenge current disease control measures (Pretty, 2008; Stoate et al., 2009) further links between various scientific disciplines are required. Blending plant genetics with epidemiology produced durable disease resistance selection (Johnson, 1984). Further blending with population genetics produced the pathogen evolutionary potential concept (McDonald and Linde, 2002; Stukenbrock and McDonald, 2008). Blending epidemiology and agronomy produced integrated crop protection against pests and diseases (Krupinsky et al., 2002). Yet, these links were developed without explicitly characterizing the efficiency and stability of the strategies. Recently, however, regarding efficiency, by decomposing population dynamics to take into account agro-ecosystem specificities control tactics could be connected to epidemiology (Bousset and Chèvre, 2012). To develop a stable management strategy to control epidemics in agro-ecosystems, a framework using evolutionary principles to define adaptation dynamics which also takes into account the specificities of agro-ecosystems would be extremely useful. Such a theory would connect disease control tactics at the different scales of the interaction between plants and pathogens.

In studies of natural ecosystems, the geographic mosaic of coevolution theory allows the adaptation dynamics, which connect scales spanning from molecules to ecosystems, to be considered (Thompson, 2005). At the individual scale, the changes to pathogenicity due to mutation or recombination on co-infected hosts, generates phenotype variability (Barrett et al., 2009; Rouxel et al., 2011). At the population scale, the average level of compatibility between the pathogen and host population is modified depending on host diversity. This diversity differentially affects a pathogen's ability for growth, multiplication or survival (Antonovics et al., 2011; Thrall et al., 2003; Laine et al., 2011). At the metapopulation scale (Hanski, 1999), the results of local interactions in time and space between host and pathogen demes determine offspring production (Laine et al., 2011). The local nature of these interactions, their differentiation and interconnection by migration produces the geographic mosaic of coevolution (Thompson, 2005). The speed of reciprocal changes in adaptation status is not uniform across space and time, leading to contrasting coevolutionary hotspots and coldspots (Thompson, 2005; Burdon and Thrall, 2009; Smith et al., 2011). The integration of these concepts, unified within a single theory, has increased our understanding of the interrelations between ecological and evolutionary processes in natural ecosystems (Thompson, 2005; Burdon and Thrall, 2009; Alexander, 2010; Laine et al., 2011), but not yet in agro-ecosystems.

Knowledge acquisition in the sciences of agricultural and natural ecosystems remains disconnected, potentially slowing down dissemination (REX Consortium, 2007). Despite the existence of pioneering work in metapopulations (Damgaard and Østergård, 1999), the adaptation of pathogens to host genetic discontinuity is still being modeled within the conceptual framework of population, without considering the impacts of fragmentation on the dynamics. In this context, fitness cost is introduced into mathematical models (Leach et al., 2001) to allow for the existence of an equilibrium state (Pietravalle et al., 2006; Sapoukhina et al., 2009). In some cases a fitness cost could be a leverage of action, especially in viruses (Janzac et al., 2009; Fabre et al., 2012) provided that the entire pathogen lifecycle is taken into consideration (Burdon and Thrall, 2008; Morris et al., 2009). However, human actions also clearly have an impact on pathogen adaptation in agro-ecosystems (Papaïx et al., 2011). While human activity alters pathogen/host coevolution (Sun and Yang, 1999), few studies explicitly include this factor in the dynamics of adaptation. Thus, the development of a conceptual framework which links these elements while taking into account the specificities of agro-ecosystems is necessary. To represent not only the effectiveness but also the stability of strategies, we believe that the theory of coevolution in the context of metapopulations can be extended and adjusted to the specificities of plant diseases in agro-ecosystems (Thompson, 2005). The objective of this paper is to adjust these concepts to agro-ecosystems to help stabilize the control of epidemics in crops using evolutionary principles. In a first step, pathogen adaptation to both resistant and susceptible hosts is formalized taking into account temporal discontinuities. Adaptation dynamics in populations and metapopulations in natural ecosystems are then compared. Next, the key points needed to adjust the metapopulation concept to the context of agro-ecosystems and represent adaptation dynamics in agro-metapopulations are described. Then, how representing these dynamics within the framework can be used to optimize the stability of epidemic control is explored. Finally, the necessary interdisciplinary collaborations and key points for research are discussed.

2. Temporal discontinuity and adaptation to two types of hosts

Unlike natural ecosystems, agro-ecosystems are characterized by the presence of humans – hereafter referred to as "actors" – whose actions and choices interfere with the development of crops and epidemics. In agro-ecosystems, agricultural practices exacerbate the homogeneities and heterogeneities in the host