Biological Control 75 (2014) 18–27

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Temporal dynamics of natural enemy–pest interactions in a changing environment

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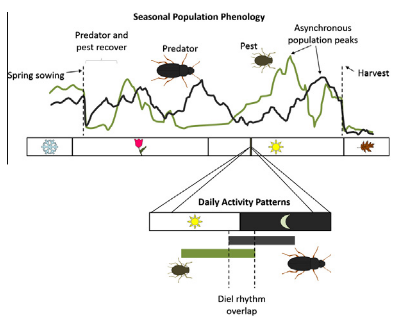
HIGHLIGHTS

- Ecosystem dynamics display cyclical oscillations on many temporal scales.
- Predator-prey interactions are mediated by their degree of temporal overlap.
- Agronomic management constrains the phenology of agrobiont organisms.
- Biological control services fluctuate with temporal dynamics of agroecosystems.
- Climate change threatens to decouple temporally-structured ecological interactions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Available online 24 January 2014

Keywords:
Population dynamics
Diel activity cycle
Predator–prey dynamics
Ecological disturbance
Climate change
Early-season predation

ABSTRACT

Agroecosystems contain complex networks of interacting organisms and these interaction webs are structured by the relative timing of key biological and ecological events. Recent intensification of land management and global changes in climate threaten to desynchronize the temporal structure of interaction webs and disrupt the provisioning of ecosystem services, such as biological control by natural enemies. It is therefore critical to recognize the central role of temporal dynamics in driving predator–prey interactions in agroecosystems. Specifically, ecological dynamics in crop fields routinely behave as periodic oscillations, or cycles. Familiar examples include phenological cycles, diel activity rhythms, and crop-management cycles. The relative timing and the degree of overlap among ecological cycles determine the nature and magnitude of the ecological interactions among organisms, and ultimately determine whether ecosystem services, such as biological control, can be provided. Additionally, the ecological dynamics in many cropping systems are characterized by a pattern of frequent disturbances due to management actions such as harvest, sowing and pesticide applications. These disturbance cycles cause agroecosystems to be dominated by dispersal and repopulation dynamics. However, they also serve as selective filters that regulate which animals can persist in agroecosystems over larger temporal scales. Here, we review key concepts and examples from the literature on temporal dynamics in ecological systems, and provide a framework to guide biological control strategies for sustainable pest management in a changing world.

1. Introduction

Agricultural fields are complex ecological communities containing intricate webs of interacting organisms. The structure and

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http://dx.doi.org/10.1016/j.biocontrol.2014.01.004
1049-9644/Published by Elsevier Inc.

function of these interaction webs are the result of a wide array of converging factors, such as weather, soil characteristics, vegetation structure and the behaviors and life cycles of the many animal inhabitants (Fig. 1). The precise manner in which these complex interacting factors converge varies over time, and this dynamic temporal component of ecological community structure, can consequently have profound effects on the biological control services provided by natural enemies within the crop. All biological phenomena are driven, at least in part, by their timing relative to other factors. It is thus important to recognize the role of temporal dynamics in structuring agroecosystems and in promoting, or limiting, the ecosystem services provided. Recent changes, both globally and locally, in climate and environmental management bring into sharp focus the importance of understanding this temporal component of biological control (Gerard et al., 2013; Thomson et al., 2010). Here, we review and synthesize key concepts and data on temporal dynamics that will provide a framework to enhance the understanding of biological control and the possible implementation of management decisions for pest suppression.

A major focus of the ecological discourse on temporal dynamics is synchrony. Synchronous events within an ecosystem are intuitively more likely to influence one another directly than asynchronous ones. In fact, many biological phenomena could not occur in the absence of precise synchrony between interacting elements. For example, nesting birds often calibrate their migration and egg-laying times to synchronize offspring hatch with peaks in the availability of food (Hegyi et al., 2013; Townsend et al., 2013; Visser et al., 1998). If this synchrony is diminished or lost due to environmental change, bird fitness and population densities can be compromised (Hegyi et al., 2013; Visser et al., 1998). Similar challenges undoubtedly face natural enemies in agroecosystems, and there is a pressing need to understand the roles of temporal dynamics in biological control. A simple truism is that natural enemies that occur at the same time as the pest can directly affect biological control, while those that do not co-occur with the pest cannot. While this seems obvious, there are nuances of the subject that remain unclear. Determining the optimal degree of temporal synchrony between natural enemies and pests is not straightforward. For example, do natural enemies have greater effects when in complete synchrony, or slightly out of synchrony, with pests? Which dynamics of the natural enemies' ecology must be in synchrony with the population cycle of the pest? With which dynamics of the pest's ecology must they be in synchrony? These are particularly pertinent questions to address from the context of shifts in environmental conditions and the consequential influence they have on biological control.

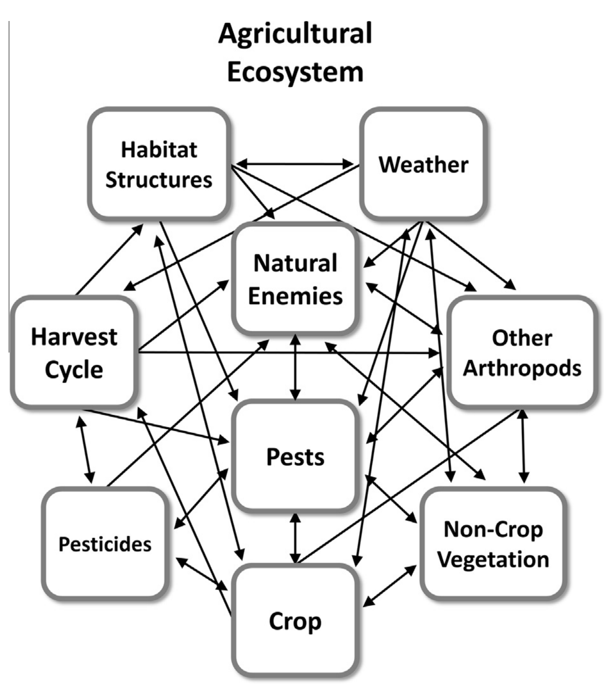

Fig. 1. Interplay between biotic and abiotic interaction webs in the agricultural ecosystem.

The definition of "synchrony" is somewhat ambiguous. When we refer to "synchrony", are we speaking of specific, discrete events as being synchronized because they occur at the same time? Conversely, are we speaking of entire cycles of interrelated dynamics that share consistent similarities in their patterns of occurrence over time? For example, adult cicada killer wasps time their emergence to maximize temporal overlap with their cicada prey (Hastings, 1986). However, to ensure regular synchrony between wasp emergence and cicada abundance over many generations, the entire life cycle of the wasp must be altered. Therefore, it is more accurate to state that the entire cycles, and not just the single events, are synchronized. No biological phenomena are isolated events and therefore selection for synchrony between two biological events invariably involves modifications to entire sequences or cycles of which the events in question constitute one part. The highly interconnected nature of ecosystems (Fig. 1) ensures that even events that are widely separated temporally have ramifications for one another; for example, the effects of ant–phorid interactions on oviposition success and later population growth of lady beetles (Hsieh et al., 2012). It is therefore important to understand the nature of temporal dynamics, not only in terms of the timing of specific events, but in the context of communities and whole suites of temporally interrelated processes.

Many biological phenomena oscillate periodically over time; that is, they occur in cycles. Familiar examples include life cycles, circadian rhythms, nutrient cycles and biochemical cycles. In fact, an ecosystem can be conceptualized as a network of interacting process cycles, and the degree of temporal overlap among the many cycles is a key determinant of ecosystem structure and function (Miller-Rushing et al., 2010; Stenseth and Mysterud, 2002). In agroecosystems, the degree to which pest populations can be controlled or regulated by natural enemies is mediated by the ability of the natural enemies to adapt to prevailing periodical cycles in the environment. The periodicity of biological phenomena imposes a regular pattern of environmental conditions and selective pressures that gradually shapes the ecology and behavior of the organisms living within a community. However, the basic properties of cyclical oscillations are rarely discussed in biological literature, so we provide here a primer to serve as a guideline for comparing and understanding temporal dynamics in agroecosystems, with a special focus on periodic oscillations and patterns. We then review the literature on temporal dynamics in biological control to highlight the central role of cyclical temporal dynamics in driving agroecology. This review therefore provides a conceptual framework surrounding predator–prey interactions within agroecosystems that can be used to guide research.

2. Cyclical temporal dynamics in ecology

The two primary characteristics of a cyclical oscillation are period and phase. The period is the amount of time required to complete the cycle once and the phase describes the position in the cycle at a given reference point in time. Both of these factors, in combination, determine which elements of an ecosystem can interact directly, and strongly influence the outcome of the interactions (Fig. 2). When the periods of two cyclical oscillations are