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Time will tell: resource continuity bolsters ecosystem services

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A common suggestion to support ecosystem services to agriculture provided by mobile organisms is to increase the amount of natural and seminatural habitat in the landscape. This might, however, be inefficient, and demands for agricultural products limit the feasibility of converting arable land into natural habitat. To develop more targeted means to promote ecosystem services, we need a solid understanding of the limitations to population growth for service-providing organisms. We propose a research agenda that identifies resource bottlenecks and interruptions over time to key beneficial organisms, emphasising their resulting population dynamics. Targeted measures that secure the continuity of resources throughout the life cycle of service-providing organisms are likely to effectively increase the stock, flow, and stability of ecosystem services.

Landscape management for ecosystem services

In the future, agriculture will need to better balance productivity with minimising negative impacts on the environment and biodiversity. One means to achieve this balance is by replacing external inputs of agrochemicals with production-supporting ecosystem services (see Glossary) generated within the agroecosystem [1]. Several key services, such as biological pest control and crop pollination, are delivered by highly mobile organisms that require management at the landscape scale to be supported [2–4]. In the past decade, landscape studies have convincingly demonstrated that the inclusion of large areas of natural and seminatural habitat in the landscape promotes species richness and overall abundance of beneficial organisms and the services they provide [5,6]. Thus, conserving remnant natural habitat provides the foundation and a minimum starting point for maintaining ecosystem services [7].

But general trends in the relationship between landscape complexity (often calculated as percentage of seminatural area in a landscape sector) and arthropod communities and services provide insufficient guidance on how to manage farms to support beneficial organisms [8]. Moreover, demand for agricultural products is high while arable land is in short supply, and it is impassable to take substantial areas of arable land out of production, converting them into seminatural habitat. We need to develop much more focused and effective means to promote service-providing organisms. We need to target the relatively few species identified as key service providers [9,10] and manage the agroecosystem to promote them based on an improved and thorough ecological understanding of the factors that govern their abundance and population dynamics.

In this opinion article, we argue for investing research efforts into identifying factors that limit the population growth of beneficial organisms. A basic principle of ecology is that the size of a population is limited top-down by predation or pathogens, or bottom-up through lack of resources [11]. We argue for, as a first step, identifying bottlenecks and interruptions over time in the chain of key resources that affect the population growth of the target organisms. Once identified, we can supply the designated resources to the agricultural landscape which we expect to more efficiently release limitations to population growth and increase stock, flow, and stability of ecosystem services, as compared with the general prescription of increasing natural habitat. The concept can be applied to any

Glossary

Ecosystem services: ecological functions provided by nature that benefit humans, for example, pest control provided by entomophagous arthropods, and pollination provided by flower-visiting arthropods that contribute to food production.
Landscape structure: type of use (composition), size, shape, and arrangement of vegetation patches and physical elements (e.g., water bodies, dwellings) in a landscape.
Life cycle: the course of developmental changes throughout which an organism passes from its inception to a mature state in which it may reproduce.
Life history: sequence of events (e.g., oviposition, pupation, emergence, and dispersal) related to survival and reproduction that occur from birth through death of an organism.
Life history characteristics: species traits that affect the life table of an organism, and include investments in growth, reproduction, and survival. Examples include gestation time, age to sexual maturity, reproductive span, life span, number of progeny or brood, and mature size.
Performance currency: a measure related to fitness (e.g., body condition, egg load) that is comparable across species and along environmental gradients.
Population dynamics: change in size and age composition of populations over time, as estimated by birth, death, immigration, and emigration.
Resource: a requirement for survival of organisms, which is often linked to the vegetation present in the habitat patch, such as plant species that provide nectar or support suitable host or prey, and shelter.
Resource bottleneck: Reduced or temporally disconnected resource that results in substantially reduced population size of the organism.
Resource continuity: the continuous availability of resources in agricultural landscapes required by a population of organisms for survival and reproduction throughout a year.
Resource interruption: Reduced or temporally disconnected resource that results in locally extinct population of the organism.

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organism or group of organisms one wishes to support. For example, figs in the rainforest provide an essential resource that enables a suite of animals to persist when other resources are unavailable [12]. Here, we exemplify the approach for mobile organisms providing ecosystem services.

Linking the resource chain

Population size is determined by the interactions of a species with the environment and with other organisms in a landscape. This process forms the basis for managing ecosystem services provided by mobile organisms such as crop pollination and biological pest control. Populations of these organisms require resources from surrounding habitats throughout a year. However, our current understanding of landscape effects on ecosystem services is largely informed by snapshot surveys of both landscapes and beneficial organisms, conducted during a part of a crop-growing season. The studies typically present summary measures of community composition and size, such as species richness and overall abundance of taxa dwelling in landscapes with contrasting proportions of arable land [5,6]. The need to move beyond the assessment of such general patterns and to link land cover types based on actual requirements for target organisms [13] and to map land cover changes over an entire season [14] are increasingly appreciated. Fahrig *et al.* [13] propose to classify land cover types to represent the resource needs of a target animal species in an agroecosystem. This approach is definitely a step in the right direction, but their framework does not explicitly consider temporal changes in resource availability. Resource continuity over time is only implicitly considered (space-for-time substitution), and clear advice cannot be provided to land managers regarding which resources will most efficiently enhance a target organism. Vasseur *et al.* [14] justifiably call for more empirical work linking the phenology and management of crops in the landscape to communities of beneficial arthropods. However, mapping changes over time in crop cover are not necessarily appropriate substitutes for actual resource needs of a target organism.

Many organisms use multiple resources in a variety of non-crop habitats [15] and the distribution in the landscape of these specific resources might not be easily linked to human-defined land cover types. For example, resources can be embedded within habitats (e.g., shaded areas or plant species that supports host prey for a target organism), which are overlooked in a course-grain land cover mapping. Moreover, a single resource can be available at different times in different habitats, such as aphid prey of arthropod predators that seasonally switch between primary and secondary host plants. For the landscape to support viable populations of beneficial arthropods, all links in their resource chain need to be present when needed throughout the entire year and not only in the crop-growing season.

Suspected resource discontinuity

Many organisms are likely to experience resource discontinuity in the form of bottlenecks or interruptions in

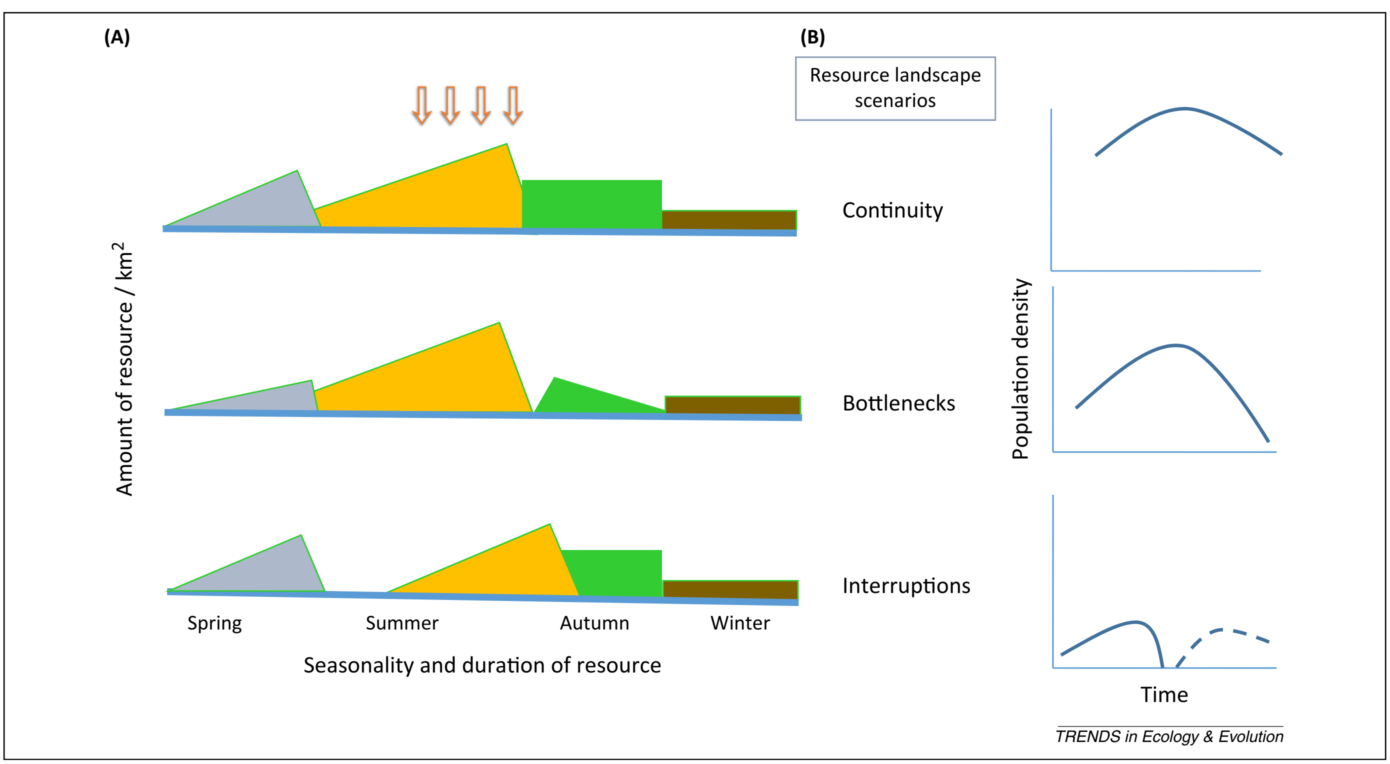

Figure 1. Scenarios of resource availability over time. Hypothetical schematic **(A)** depicting resource amount (per km^2; '*y*' axis), against time of year when available, and duration (X axis). Examples show resource continuity (top), discontinuity as bottlenecks (middle), and as interruptions (bottom), as related to the resource needs of a target organism. Panel **(B)** depicts implications for population dynamics for each respective resource situation. Colours represent types of resources. The top left continuity example shows resources to be available throughout the year, although in different amounts, and corresponding population densities (top right) are sustained at high and more constant levels. The bottleneck and interruption scenarios exemplify extreme limitation or absence of resources, respectively; peaks in population densities will be lower and changes in density will occur faster. The four arrows represent the sampling period of data collection of typical snapshot landscape ecology studies.