Opinion

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

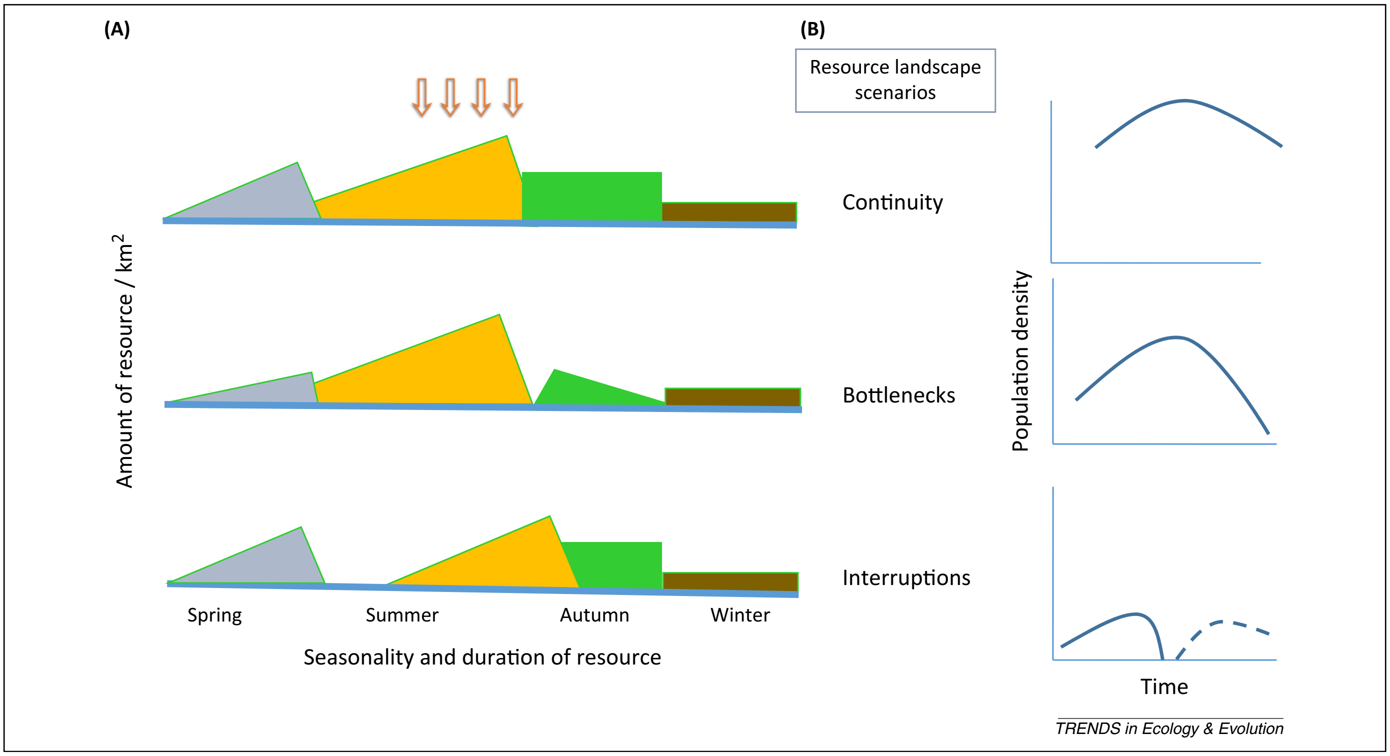

Figure 1. Scenarios of resource availability over time. Hypothetical schematic **(A)** depicting resource amount (per km^2; '*y*' axis), against time of year when available, and duration (X axis). Examples show resource continuity (top), discontinuity as bottlenecks (middle), and as interruptions (bottom), 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.

current agricultural landscapes (Figure 1). Periods of resource scarcity can lead to failure to support an entire generation or a particular life stage. Beneficial arthropods, such as flower-visiting insects, predatory spiders and insects, and parasitic flies and wasps, move over large distances, live for several months or years (e.g., [16,17]), and need multiple resources to complete their life cycles. These resources can include various foods, shelter, nesting sites and materials, or overwintering sites that extend well beyond the often ephemeral, albeit abundant, resources provided when a crop flowers or a pest breaks out [2,7]. It is, thus, well recognised that the availability of multiple resources and maintenance of resources are crucial for the fate of organisms supported in agricultural ecosystems. Despite this, there is little research explicitly exploring the importance of resource availability for populations of beneficial species throughout a year.

We can surmise from information of the resource needs through the life cycle of an organism that resource bottlenecks and interruptions are likely to occur in intensively managed landscapes. From compilations of resource needs and sequential seasonal movements of the predatory lady bird beetle, *Coccinella septempunctata* (L.) in Bohemia [18] (Figure 2A), it is probable that despite their high mobility, lady beetles experience resource bottlenecks or interruptions in intensively cultivated regions where landscapes are dominated by ephemeral and changing cropping systems. For instance, an agricultural production system oriented towards biofuel can result in a landscape dominated by maize and can be hypothesised to lead to resource interruption for lady beetles attributable to lack of habitat for reproduction early in the season (Figure 2B). Hence, population density is likely to decline.

In the subtropical regions of eastern Queensland Australia, arthropods are active year round in landscapes dominated by summer- (e.g., cotton, sorghum, beans) and winter- (e.g., wheat, barley, chick peas) growing crops. However, there is a 6- to 8-week gap in autumn when summer crops are harvested (in late April to June) and winter crops are being planted. This gap is a critical time when beneficial arthropods are active and resources might be interrupted to the demise of their populations [4,19]. Thus, even in diverse agricultural landscapes, for example, with high proportion of forest and grassland or a diversity of crops, that are considered to harbour all necessary resources, events of resource interruptions and bottlenecks can occur [20,21].

Demonstrated resource discontinuity

There is little hard evidence demonstrating the causal link between sufficient resources and enhanced population abundance of a beneficial organism. Availability of overwintering habitat in the form of perennial grass margins has been shown to enhance local populations of ground-dwelling predatory arthropods colonizing annual crops [22], but whether or not this habitat is related to the release of a resource limitation or to other factors that regulate population size remains unclear. An analysis of survival, foraging success, and reproduction throughout the life cycle of a dominant ground beetle in Sweden suggests that lack of food before and after the crop-growing season (when the crop pest is not present) provides a bottleneck hampering population growth in landscapes with little perennial habitat [23].

In a unique study, Corbett and Rosenheim [24] hypothesised that planting French prune trees adjacent to vineyards

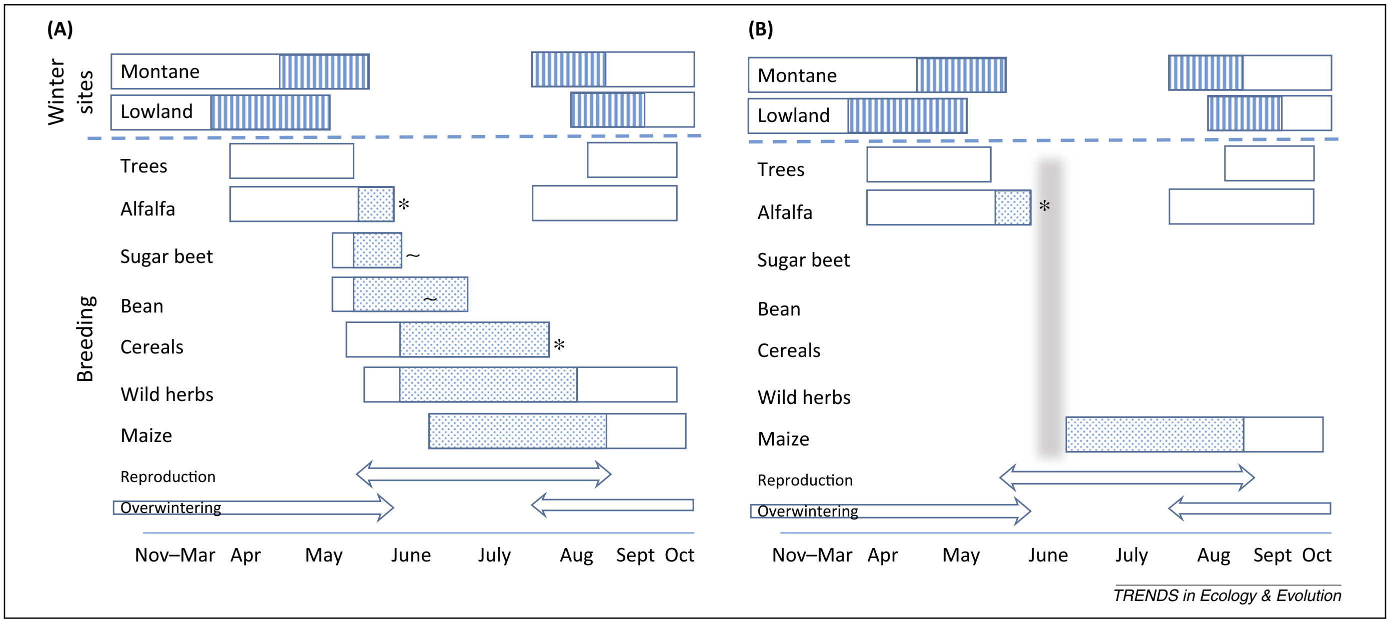

Figure 2. Seasonal habitat use. A schematic of **(A)** seasonal habitat use by the aphidophagous lady bird beetle, *Coccinella septempunctata*, in agricultural landscapes in Bohemia, central Europe (redrawn, with permission, from [18]), and **(B)** hypothetical landscape dominated by maize with some alfalfa, which would result in a resource bottleneck and interruption early in the season as *C. septempunctata* leaves its overwintering sites (indicated by the vertical grey shading). Other production landscape scenarios of resource bottlenecks and interruptions can be imagined, for example, a landscape dominated by oilseed rape and cereals would leave late-season resource bottlenecks, regardless of the amount of forest. Striped parts of the bars in 'winter sites' indicate periods of immigration and emigration from overwintering sites. Horizontal bars indicate the presence of lady bird beetles in habitats, stippled areas indicate breeding periods. Disturbance is indicated by '*' for mowing or harvest, and '~' for insecticide use, both of which can result in resource bottleneck and interruption. The horizontal arrows indicate the period of potential reproduction and overwintering of the beetle.

can provide off-season habitat requirements for *Anagras* spp. parasitoids on grape leafhopper pests, *Erythroneura elegantula* (Osborn), in Californian vineyards. They used rare element labelling to confirm that overwintering refugia for the parasitoid on French prune enhanced early season colonisation in the vineyards. The trees harboured alternate hosts, thereby providing resource continuity for the parasitoid and an option for effective biological control management.

Another graphic example is provided by bumble bees (*Bombus vosnesenskii* Radoszkowski and *Bombus terrestris* L.), that are abundant pollinators in flowering crops, especially across the northern hemisphere. Early in spring, the queen of these social bee species establishes a nest in which she first produces workers that forage in the surrounding landscape. Later in the season she switches to produce males and gynes that carry the next generation. Early-season mass-flowering crops, such as oilseed rape, enhance the bumble bee population, but lack of resources later in the season limit reproductive success and thereby population growth between years [21,25]. Planting even small areas of late-blooming flowers, such as red clover, markedly enhanced the abundance and reproductive success of bumble bees in the landscape, clearly a result of releasing a resource bottleneck [26].

These examples illustrate how research focused on retrieving detailed information on needs, continuity, bottlenecks, and interruptions of resources, and the effect on population regulation of beneficial organisms will allow us to efficiently design landscapes such that resource limitations are released. Doing so, new limiting factors will appear, top-down drivers might also arise, for example, natural enemies of the beneficial organisms, (e.g., parasites of pollinating insects [27] and parasitoids and predators of biological control organisms [28]) might be promoted by the resource release, and the services that they provide might be disrupted. Non-target organisms might be affected and even pests can be enhanced by the measure. The resource-release intervention needs to be tested in real landscapes and followed up with monitoring of impact on target and non-target populations and services.

Research agenda

We need to gather detailed information of the life-stage requirements of the organisms we decide to support. This, together with the spatiotemporal distribution of these resources, will allow us to pinpoint resource (dis)continuity in the landscape. There is ample general information on the life cycles and life history stages of the often cosmopolitan beneficial arthropod predators, parasitoids, and pollinators that dwell in crop fields. Much of this information is based on natural history observations. However, quantification of their locations, abundances, and actual resource requirements inside and outside the crop field throughout their life cycle are only beginning to be conducted [21,29,30].

We suggest a research agenda in which resource continuity in the landscape is identified in four steps. The first step is to identify phenological sequence of the target organism recognised as an efficient service provider and the type of resource necessary for each life stage, such as requirements for overwintering and nesting, and host or food species. The second step is to quantify the amount and quality of resource per unit area within the dispersal range of the target organism and in the surroundings of the crops requiring service provisioning. Because the resources are not necessarily tightly linked to habitats or land cover types as we define them, this step is likely to require empirical assessments of the distribution of resources in the landscape. The third step is to estimate the seasonality and duration of the resources. When linked to the life-cycle requirements of the target species, this will reveal how well the availability of resources match critical times in the life cycle affecting the fitness and population build-up of the species throughout the year. This matching is crucial for the identification of resource bottlenecks and interruptions, because an abundant resource which can last for a long time, but is asynchronous with the needs of the species, or is abruptly ended (e.g., at harvest or grazing) will contribute little to the performance in terms of population growth. Whether a temporal mismatch between resource availability and requirements will result in substantially reduced population size (bottlenecks) or in local extinction (interruptions) depends on the characteristics of the organism and its ability to survive poor conditions, for example, through migration or diapause [31]. Finally, we can, based on the acquired information, develop hypotheses and ideas for targeted measures that in turn need to be tested and evaluated in field experiments (Box 1).

Suggestions for practical steps

In practical terms, there are several approaches to identify resource discontinuity as related to each life stage. One is to measure resource availability and changes in population size or demographic rates (birth, death, and growth rates) at multiple scales on all resources that the beneficial organism needs across habitats and seasons throughout the year. This is informative, but costly in labour and time and should be preceded by an identification and study of a subset of situations likely to show resource limitation. A more parsimonious approach is to collect information on the requirements of the species and match that to information on resource abundance and seasonality from the literature, expert opinion, and local knowledge. This baseline can be supplemented with experiments, and targeted observations, and then extended spatially and temporally using geographical information systems and remote sensing. The information can be summarised in a diagram or digital map to depict the spatial scale and timing of resource use in the life cycle of one or more species [32]. On the basis of this information, hypotheses on resource bottlenecks can be formulated. Before they are tested in experiments it is efficient to first test them *in silico* through sensitivity analyses or scenario projections in general population models that demand relatively few estimated parameters (e.g., [33,34]).

The hypotheses then need to be tested in nature. One approach is to select landscape sectors in the region that reflect scenarios of continuity, bottleneck, and interruption (Figure 1, left), and in these estimate changes in population abundance or demographic rates over the year

Box 1. Future research directions

<table>
<tr><th>Go beyond:</th><th>To ask:</th></tr>
<tr><td>‘How complex is the landscape structure?’</td><td>‘What is the collection of resources needed for all life stages of beneficial arthropod species, and how continuous are these resources?’</td></tr>
<tr><td colspan="2">The trend is clear, complex landscape structure support higher abundance and species richness of natural enemies [5,45], and seminatural habitat and floral resource enhances pollinators [46,47]. However, we know little about which resource type beneficial arthropods need to link life cycle with annual population cycle.</td></tr>
<tr><td>Go beyond:</td><td>To ask:</td></tr>
<tr><td>‘How abundant and species rich are beneficial arthropod communities along a snapshot landscape-resource gradient?’</td><td>‘How does population size, demographic rates, or measures of performance currency of key ecosystem service providers change when the resource chain is broken?’</td></tr>
<tr><td colspan="2">The population growth and life-history characteristics of beneficial organisms can be affected by discontinuity of resources [30,48]. Several examples suggest that adding the right resources to the landscape can target organism performance and enhance population size of organisms that deliver pest suppression and pollination. The continuity of resources across a year might help maintain body condition and reproduction of organisms, even in landscapes that are simple and intensively managed. Ground beetles overwintering in ley habitat had good body condition and egg loads [23]. The timing of predator arrival is as important as landscape complexity for mediating pest control in agroecosystems [49]. Poor spring and autumn floral resources result in poor fitness of bees [21,50].</td></tr>
<tr><td>Go beyond:</td><td>To ask:</td></tr>
<tr><td>‘How does spatial heterogeneity affect arthropod trophic structure?’</td><td>‘How does releasing the resource bottleneck affect trophic structure and flow of ecosystem services?’</td></tr>
<tr><td colspan="2">Gradients of spatial heterogeneity affect community structure and organisms are sensitive to changes in habitats that restrict food or structural resources [2,51]. Depending on the life stage of the organisms or the trophic level, for example, hyperparasitoids versus primary parasitoids, limited or interrupted resources can affect populations and communities differently [52,53].</td></tr>
<tr><td>Go beyond:</td><td>To ask:</td></tr>
<tr><td>‘How does landscape heterogeneity and farming practice interact?’</td><td>‘How does resource continuity buffer communities from disturbance (e.g., tillage, pesticides, crop harvest)?’</td></tr>
<tr><td colspan="2">We now know that landscape heterogeneity and farming practices interactively influence the taxonomic and functional composition of beneficial arthropod communities, and in some cases the services that they provide [54–58]. Improved understanding of the extent to which management interventions, such as improvement of resources within crop habitat (at multiple spatial scales [59]), but also outside crops, buffer communities from disturbance events is needed [60].</td></tr>
</table>

(Figure 1, right). A scoping exercise, that should be possible to perform with plenty of available data, is to statistically relate the local population size to the functional composition (as defined by the resource demands of the organism) of the surrounding habitats [13]. For instance, habitats available to a population of a pollinating insect can, based on measurements or expert opinion, be characterised by resources, such as flower and nesting site density, resource seasonality, such as phenology of duration bloom, and frequency and timing of disturbances, such as harvesting, tillage, and pesticide treatments. Furthermore, these habitats can be weighted by the amount of each resource that is embedded. Techniques developed for analysis of functional traits for species [35,36] can be employed to investigate which of these habitat characteristics is limiting the beneficial organisms.

Another option is to add a defined resource to the landscape, for example, an early or late mass-flowering crop to bumble bees, and compare population responses in landscapes with more, less, or none of that resource. For measuring impacts of such directed resource additions on a population, we need to go beyond snapshots of species abundance and distribution. Instead, changes in population size need to be continually tracked over the year, and across the landscape sectors [25], not only in the habitat with the added resource. In addition, it is possible to measure population responses associated with population growth (births, deaths) of individuals or colonies [21,26], and population responses associated with movement (immigration, emigration [15,37]). Demographic estimates are vital statistics underpinning population dynamics that can be used to identify how resource conditions drive population decline or increase over time. However, as they are difficult to estimate for many organisms, they can be substituted by a performance currency related to the acquisition of energy and nutrients such as body size, fat contents, per capita reproduction, and occupancy and survival at critical times in the year. The collected information can feed into and continually improve models of resource and beneficial arthropod population dynamics for testing scenarios of resource bottlenecks and interruptions. Several models have been developed that can be calibrated to reflect regional conditions and continually extended to explore and predict the impacts on beneficial arthropods and services in a changing world for biological control [38] and pollinators [2,39].

Concluding remarks

The high demands for agricultural products and lack of arable land will allow for relatively small management interventions for ecosystem services in the production landscape. Most current snapshot studies on spatial heterogeneity suggests maintaining 17–40% seminatural habitat in intensively cultivated landscapes to tangibly enhance the delivery of pollination and pest control services [40–43]. This is unlikely to be implemented in most agricultural landscapes. Furthermore, agricultural landscapes are dynamic and will change in land cover as a result of shifting demands for agricultural products and public goods, such as carbon sequestration, clean water, biodiversity conservation and recreation, further habitat loss and fragmentation, and adaptations to climate change. Approaches to support ecosystem services via the satisfaction of resource demands for service providers must also be adaptable, continually updated, and align with and take advantage of constantly changing crop production systems. This responsiveness can only be achieved if we first gain a comprehensive understanding of the ecological mechanisms that drive changes in abundance of beneficial arthropod populations in agricultural ecosystems. If we do not bother to learn about these mechanisms, acknowledging that ecosystem services are based on dynamic processes, ecological research will fail both to predict the impacts of global change and to lead the development of efficient land-use practices that reinforce ecosystem services in a changing environment.

Researchers aiming to understand and promote ecosystem services provided by biodiversity need to embrace the temporal dimension of abundance and resource dynamics in their landscapes [14,44]. But to achieve this we will not have to reinvent the wheel, nor depart from known tracks. We should appropriate the historically extensive research on population regulation for the new research challenges (Box 1). Building on the attained knowledge from landscape ecology and adding to these considerations of resource variation and population regulation over time will allow us to develop targeted and efficient ways to release limitations to growth of beneficial organisms and enhance the flow and stability of ecosystem services to agriculture.

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