Designing agricultural landscapes for arthropod-based ecosystem services in North America

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Abstract

Agricultural landscapes in North America have developed through complex interactions of biophysical, socioeconomic and technological forces. While they can be highly productive, these landscapes are increasingly simplified, causing biodiversity loss. As a result, ecosystem services associated with biodiversity are being dismantled. Agricultural landscape structure arises from collective decisions of farmers over long time periods, which are usually not intentionally coordinated beyond the farm scale. Regaining ecosystem services will require active efforts to intentionally redesign landscapes, in part based on ecological evidence about relationships between landscape structure and ecosystem services. Here we focus on services provided by arthropods and how to foster them at landscape scales. We first provide a brief history of how agricultural landscape structure in temperate North America developed and review the landscape-scale ecological drivers underpinning arthropod-based ecosystem services. We then propose ecological and social principles for designing agricultural landscapes, based on the ecological evidence we reviewed and on previous efforts in agricultural landscape design. Finally, we look ahead to discern prospects for putting agricultural landscape design into practice, including ecological, technological and policy opportunities. To reap benefits from arthropod-based services, future agricultural landscapes will need to increase in structural heterogeneity and diversity across multiple dimensions including crop, farmer and consumer diversity. A number of knowledge gaps persist, including how to design landscapes at spatial scales that are relevant to service providers, identifying areas of overlap or conflict between design for ecosystem services and for biodiversity conservation more broadly and navigating the social and political processes needed to implement landscape design.

Keywords: landscape design, pollination, pest suppression, agricultural policy, principles, ecosystem services

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Outline

1. **Introduction**
2. **A brief history of agricultural landscape structure in temperate North America**
3. **Arthropod-based ecosystem services in agricultural landscapes**
    a. *Pest suppression*
    b. *Pollination*
    c. *Decomposition & nutrient cycling*
    d. *Additional services*
4. **Ecological drivers of arthropod-based services**
    a. *The critical role of biodiversity*
    b. *Resources for service providers in agricultural landscapes*
    c. *Spatial heterogeneity at landscape scales*
    d. *Temporal heterogeneity within and across seasons*
5. **Principles for ecological design of agricultural landscapes**
6. **Opportunities for putting design into practice**
    a. *Crop diversity*
    b. *Grower and consumer diversity*
    c. *Conservation programs*
    d. *Technology-based opportunities*
    e. *Climate change*
7. **Conclusions**

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1. Introduction

A key challenge for humanity is to develop agricultural systems that support a growing human population, minimize negative environmental impacts and are resilient to global change. The scope of this endeavor is massive, as farmland now occupies around 40% of our planet's terrestrial surface (Foley et al., 2011) and agriculture is the driving factor shaping landscapes in many regions. We have successfully boosted crop yields over the last several decades (FAO, 2020), a feat achieved primarily through agricultural intensification. Intensified agriculture uses high-yielding—but increasingly homogeneous—crop varieties, which are usually grown in expansive monocultures and require high levels of irrigation, chemical fertilizers and pesticides (Matson et al., 1997). Unintended results of agricultural intensification include unacceptable levels of greenhouse gas emissions, disruptions to global N and P cycles (Bouwman et al., 2013; Glibert, 2020) and biodiversity loss (Dudley and Alexander, 2017; Flynn et al., 2009; Wagner, 2020). In many regions, the unsustainable nature of these intensified systems—including environmental, economic and social dimensions—has become even more starkly evident in the context of the COVID-19 pandemic, prompting calls to re-envision multifunctional landscapes that strengthen the resilience of rural communities (Prokopy et al. 2020).

The products we derive from agriculture—food, feed, fiber and fuel—are underpinned by a complex set of supporting and regulating ecosystem services that depend on biodiversity (Zhang et al., 2007; **Box 1**). For example, soil microbes and invertebrates lay the foundation for agriculture by governing formation of soil organic matter; they also regulate nutrient loss from soils and uptake by plants (Bender et al., 2016). Other organisms, both invertebrates and vertebrates, regulate essential processes like pollination and suppression of crop pests, although they can also contribute to crop losses via herbivory and disease transmission (Lindell et al., 2018; Peisley et al., 2015; Saunders et al., 2016).

Intensified agricultural practices can suppress or eliminate service-providing organisms that live in and around crop fields while disservice providers (i.e., pests) persist. Many service-providing organisms depend on resources found in other habitats outside of crop fields (e.g., Schweiger et al, 2005; Wood et al., 2018); the simplified landscapes that result from agricultural intensification often lack these habitats. This means that intensification, while it has been a successful means to increase global yields in the short term, undermines agriculture by eroding the biodiversity-mediated services on which it depends (e.g., Bennett et al., this issue; Vanbergen et al., this issue). These services are instead replaced by external inputs—for example, using insecticides instead of relying on natural enemies for pest suppression (Meehan et al., 2011; Meehan and Gratton, 2016, Paredes et al. 2020)—but economic and ecological costs of this approach are high and will continue to grow (e.g., Burkart & James, 1999, Siebold et al., 2019). Intensification also incurs social costs pertaining to inequities in who is capable of participating in agricultural development and who benefits (Abson, 2019). To counter the negative impacts of intensification, we need to design and intentionally foster conditions that allow ecosystem services to increase (Landis, 2017).

Agroecologists and others are developing strategies to make agriculture more conducive to biodiversity and to promote the ecosystem services that biodiversity provides. The concept of leveraging ecosystem services toward increasing yields, rather than relying on external inputs, is sometimes referred to as ecological intensification (Kleijn et al., 2019; Tittonell, 2014). Most research on ecological intensification focuses on practices that promote biodiversity and ecosystem service provision at the field-scale, i.e., decisions farmers can use within a single crop field about tillage, pesticide use, intercropping and so on.

These are critically important and are reviewed elsewhere (Hole et al., 2005; Kremen and Miles, 2012; Lichtenberg et al., 2017; Muneret et al., 2018).

Here, we focus specifically on spatial scales that are broader than a single field: the landscape-scale. Agricultural landscapes include multiple habitat types, including patches of crop fields and various other vegetation types. These can occur within individual farms, as many operations contain multiple crop fields, hay fields, woodlots, fallow areas, etc. They also occur at the scale of multiple farms and the uncultivated spaces in between, which in aggregate form the broader agricultural landscape. Thus, a mosaic of cropped and less-managed uncropped areas such as roadsides, fallow fields, hedgerows, wetlands, perennial grasslands, woodlots, etc.—often collectively referred to as "semi-natural habitats" —forms the agricultural landscapes that we manage.

A key lesson from landscape ecology is that processes at a given location are influenced by characteristics of the surrounding landscape (Tscharntke et al., 2012). In an agricultural context this means that levels of biodiversity, ecosystem services and even yields in a given crop field are partly functions of nearby land covers and land uses, in addition to within-field practices. Therefore, in order to maximize levels of biodiversity and associated services we must be concerned not only with field-level management, but also with the makeup and spatial arrangement of the broader landscape (**Fig. 1**). Agricultural landscape structure emerges from the combination of many individual management decisions. These decisions are often quite logical from the perspective of individual growers but typically are not coordinated between farms that share a landscape. It follows that agricultural landscapes tend to develop without intentional design, or alternatively that they have been indirectly designed by economic and policy forces that are not concerned with environmental outcomes or ecosystem services (Jackson, 2008; Liebman and Schulte, 2015).

The value of coordinated landscape-scale design has long been recognized, but has occurred mostly in cities. Urban designers and planners seek to improve human welfare by coordinating how transportation, buildings, parks, etc. are configured (Hall, 2014). Similar approaches should be applied to consciously re-designing agricultural landscapes to harbor biodiversity and maintain critical ecosystem services, a task which will require stakeholder involvement in coordination and planning (Landis, 2017; Nassauer and Opdam, 2008). However, compared to urban design, agricultural landscape design is an underdeveloped concept. We define agricultural landscape design as the process of intentionally planning and shaping the landscapes where farming occurs toward a defined goal or outcome. Designing landscapes specifically for ecosystem services, which is our focus here, has the goal of structuring landscapes to conserve beneficial species and promote the ecosystem services they deliver. This is related to, but also somewhat distinct from, designing landscapes for biodiversity conservation *per se* (**Box 2**).

In this chapter, we review relationships between agriculture, landscape structure and ecosystem services (**Fig. 2**), with a focus on the temperate portions of North America. Our aim is to share evidence that points toward general principles for intentionally designing agricultural landscapes that maintain sufficient food production while minimizing the costs of intensification. While taxa ranging from birds (Sekercioglu et al., 2016; Whelan et al., 2008) to microbes (Brussaard et al., 2007; Verma et al., 2017) can be important service providers, we focus on services involving arthropods, as these organisms are our area of expertise and tend to be some of the most ubiquitous, diverse and important for key agricultural processes. In an effort to make this review accessible to non-specialists, we provide brief overviews of the history of agricultural landscapes in North America (section 2) and the variety of arthropod-based ecosystem services in agricultural landscapes (section 3a).

2. A brief history of agricultural landscape structure in temperate North America

The physical structure of agricultural landscapes develops over time as a result of complex interactions between biophysical and social factors (**Fig. 2** orange box). The underlying physical geography of a landscape creates initial parameters (e.g. topography, soils, water bodies) which influence subsequent human choices. In North America, Indigenous peoples conducted varied forms of agriculture for millennia which extensively altered the landscape (Denevan, 1992; Mt. Pleasant, 2015). However, infectious diseases carried by European colonists, followed by genocide and systematic relegation of Native populations to marginal lands through so-called "Indian removal" devastated Indigenous communities and cultures (Dunbar-Ortiz, 2014; Hinton et al., 2014), and natural succession had largely concealed evidence of Indigenous farming by the 1800s (Denevan, 1992).

As colonization and westward expansion progressed, the system used to define units of lands available for claim, sale, or purchase left a lasting imprint on landscape structure. For example, in the Eastern U.S. the 13 original colonies were laid out using the British Metes and Bounds system (Brady, 2019). This system relies on pre-existing physical features (rivers, streams, previously established trails, etc.) which often do not follow linear patterns. As a result, agricultural fields in the Eastern US are often irregular in size and shape (**Fig. 3a**). In contrast, in much of the U.S. Midwest and West, land was surveyed during the 19th century using the Public Land Survey System (also known as the Rectangular Survey System; White, 1983). Surveyors established an east-west 'baseline' and an intersecting north-south 'meridian' from which many subsequent boundaries were determined. The highly rectangular patterns of fields and woodlots in the Midwest are a legacy of this system (**Fig. 3b**).

Agricultural landscapes also inherit a great deal of their structure from evolving technologies. Introduction of the moldboard plow for breaking up native prairies catalyzed the almost complete conversion of these ecosystems in the Midwest to crops (Bogue, 2011; Smith, 1981). Further west, the invention of barbed wire to control cattle was instrumental in bringing agricultural activity to the Great Plains during the late 19th century (Netz, 2004). This westward expansion, combined with industrialization in the east, contributed to a "forest transition" in New England, where widespread abandonment of agricultural land and reforestation occurred (Mather 1992).

Technologies also developed to deal with deficits or excesses of water. In the arid West, large federally-funded irrigation projects beginning in the early 20th century impounded or diverted waterways in order to "reclaim" land for agriculture (Stern and Normand, 2020). In the following decades, advances in irrigation technology like high-powered well pumps and center-pivot irrigation systems allowed farmers to exploit aquifers much more effectively, greatly increasing the footprint of cultivated land in the American West (Green, 1981).

Some areas of the Midwest had very high water tables and abundant wetlands. Farms in these regions frequently contained areas that were spared from cultivation because they were too wet; however, since the mid 20th century, flexible plastic drainage systems have been replacing clay and concrete ones

(Pavelis, 1987). Since these are cheaper and easier to install they have allowed for further expansion into wet soils that were previously left uncultivated.

While such technological advances initially reduced the area under cultivation in some regions (i.e. New England), this was largely offset by agricultural expansion and intensification in others (Ramankutty et al. 2010). In these key crop-producing areas, industrial agricultural technologies have exacerbated landscape simplification by dictating the size, shape and layout of crop fields. In a process likened to a treadmill (Cochrane, 1958; Levins and Cochrane, 1996), farmers adopt new (and often larger) tools that reduce the cost of production, increasing the total amount of crop grown. This in turn drives prices down, creating further pressure both to cultivate more land and to make considerable investments in new technologies when they come up in order to remain competitive. This cycle, abetted by economic and policy drivers, is implicated in the general trend toward consolidated farm ownership and the simplification of landscapes. Resulting in part from this dynamic, the trend in the United States has been toward fewer farmers operating more acres each, with larger farms subsuming smaller ones. For example, in 1987, half of all harvested land in corn was on farms that were 81 hectares (200 acres) or smaller. A quarter-century later, in 2012, this midpoint had more than tripled to 256 hectares. All other major crops in the US—soy, wheat, cotton and rice—have followed similar trends and at least doubled in midpoint area, as have most minor field crops (MacDonald et al., 2018).

In many landscapes, common features like fencerows, hedgerows and hay fields have been lost to intensification. Before tractors were widely adopted in the mid 20th century, farms had animals (horses, cattle) that required grasslands for grazing or hay along with some means of confinement. In some cases, farmers adapted European methods for creating hedges of living plant materials to confine animals (Smith and Perino, 1981), while in others wooden, stone or metal fencing was erected (Thorson, 2009). Field and property boundaries often contained trees that were spared from forest clearing, or unmanaged vegetation that was allowed to grow up afterwards. While far from pristine, these semi-natural habitat features provided relatively biodiverse and perennial linear habitats bordering annual crop fields. In many areas they are still characteristic of agricultural landscapes (**Fig. 3c**). However, as crop and livestock production became more concentrated and spatially segregated and farm implements became capable of covering larger areas, these features were often removed. Fencerows, hedgerows and hay fields, along with the biodiversity they supported, have disappeared from many agricultural landscapes and been replaced with a small number of annual crops grown in increasingly large fields (e.g., **Fig 3d**; Vance, 1976; White and Roy, 2015).

Finally, crop production has undergone dramatic spatial segregation, causing crop diversity within landscapes to plummet (Crossley et al., 2020). Until the mid 20th century, many crops were grown widely, as they were often bought and sold locally or used on the farm (e.g., farmers grew grain and hay to feed their own livestock, and other types of produce needed to be marketed quickly before they could spoil). However, longer supply chains and subsidized transportation infrastructure have allowed crop production to become spatially concentrated with particular regions specializing in a very small number of crops. Some of this tight clustering has occurred quite recently; Crossley et al. (2020) found the spatial concentration for 13 of 18 major crops in the US increased 15-fold from 2002 to 2012. This spatial reorganization has led to strong contrast between regions in terms of which crops are produced and means landscapes that formerly contained many crop types are now much more homogeneous.

In summary, agricultural landscapes in North America reflect a confluence of physical geography, colonial history, agricultural policies and technology, and have become increasingly intensified and simplified. Many characteristics of these landscapes have arisen without coordinated planning and those efforts that have entailed landscape-scale planning (e.g., surveying, drainage and irrigation) were focused on increasing cultivated land area with little regard for how it influences landscape structure or biodiversity.

3. Arthropod-based ecosystem services in agricultural landscapes

The livelihoods and well-being of people often intersect with the populations and activities of arthropods in agricultural landscapes. In fact, arthropods have the potential to influence virtually all of the United Nations' sustainable development goals (Dangles and Casas, 2019). As dominant organisms in terrestrial ecosystems, arthropods provide a wide range of ecosystem services (**Box 1**, **Fig. 2** blue box) affecting processes and outcomes such as the consumption of pests by natural enemies, pollination of crops and the maintenance of soil fertility by decomposers.

3a. Pest suppression

An important process that arthropods carry out is the consumption of other insects and plants, some of which are considered pests by people. Crop losses from herbivorous insects worldwide are estimated to be 18-20% (Sharma et al., 2017). Predatory arthropods include taxa like spiders (Araneae), ground beetles (Coleoptera), true bugs and wasps that can be voracious and important predators and parasitoids of crop pests. Predation and parasitism can be leveraged intentionally in the form of biological control programs, which can decrease overall insect pest abundances 130% more than control groups (Stiling and Cornelissen, 2005). However, natural pest suppression also occurs without human intervention, as unmanaged predators and parasitoids that occur in a landscape find and consume crop pests. Economic valuations of natural pest suppression vary by crop and spatial extents (Zhang and Swinton, 2012), but early estimates placed their value at $4.5 billion per year in the United States (Losey and Vaughan, 2006). A recent meta-analysis by Naranjo et al. (Naranjo et al., 2019) estimated that natural pest control contributes on average $74 per hectare to crop production, with high-value horticultural crops benefiting more than field crops and habitat management schemes providing more value than other conservation strategies, though they note good examples are limited.

Arthropods also contribute to weed suppression via herbivory and seed predation. Biological control of weeds using insects has frequently been successful for invasive weeds in natural settings (van Driesche, 2012) while biocontrol of weeds in arable crops is more difficult (Müller-Schärer et al., 2000). As recently reviewed by Sarabi (2019), in arable crops, arthropods primarily help to control weeds by acting as seed predators. Feeding on developing seeds on plants, termed predispersal seed predation, is considered the most important form of seed predation and is carried out by many types of arthropods, including flies, beetles, wasps and larvae of butterflies and moths. After weed seeds have ripened and been released into the environment, they are frequently fed on by ground beetles, ants and crickets resulting in post-dispersal seed predation. The effectiveness of seed predation in arable crops is influenced by field management practices and landscape context (Landis et al., 2005; Petit et al., 2018) and can result in significant reduction in weed seed banks across multiple cropping systems (Bohan et al., 2011).

3b. Pollination

Another group of arthropods that provides valued functions are pollinators. Several orders of insects visit flowers to feed on nectar and pollen, and in the process transfer pollen between flowers, allowing fertilization and seed production to occur. Worldwide, between 78 and 94% of flowering plant species require some form of animal pollination (Ollerton et al., 2011). As much as 70% of the plant species used for food by people and about one third of global crop production depend to some degree on animal pollination (Klein et al., 2007), and these plants contribute as much as half of the essential vitamins to our diets (Chaplin-Kramer et al., 2014; Eilers et al., 2011; Smith et al., 2015). Much attention is placed on bees, which are perhaps the most important group of pollinators, but other insect groups also contribute (Rader et al., 2016). These include hoverflies (Diptera: Syrphidae), soldier beetles (Coleoptera: Cantharidae) and moths and butterflies (Lepidoptera). Though there are various ways in which the contributions of insects to agricultural production can be valued (Winfree et al., 2011), estimates from global datasets suggest that the economic value of pollinators to crops was over US $200B in 2005 (Gallai et al., 2009) and in 2015 pollination had an annual market value of $235B - $577B, or 5-8% of global crop production (Potts et al., 2016). A recent analysis found that 5 out of 7 pollinator-dependent crops studied in North American agroecosystems showed evidence of pollinator limitation, suggesting that enhanced pollinator communities in these landscapes could improve yields (Reilly et al., 2020).

3c. Decomposition & nutrient cycling

Invertebrates also contribute to decomposition and nutrient cycling in agricultural landscapes, serving as important facilitators (Culliney, 2013; Neher and Barbercheck, 2019) and indicators (Menta and Remelli, 2020) of soil health. For example, isopods (woodlice), myriapods (millipedes), collembola (springtails) and several groups of mites (e.g., orabatids) are important in influencing nutrient mineralization (De Ruiter et al., 1993) and, to a lesser extent, carbon flows in soils (Grandy et al., 2016), both critical determinants of soil quality and plant productivity. For example, in laboratory experiments Joly et al. (2018) found that conversion of ingested leaf litter to feces by a common millipede resulted in increased C and N mobilization relative to intact litter. Similarly, field experiments have shown dung beetle activity has positive effects on soil nutrient availability and ultimately plant growth (Doube, 2018; Wu et al., 2011). Dung burial also results in decreased fouling of forage, reduced N volatilization and reductions in pest flies, estimated as saving $380M in economic losses (Losey and Vaughan, 2006). Despite documented examples of how arthropods influence soil processes, studies also show significant heterogeneity in ecosystem responses to the activity of decomposers. The potentially important effects of abiotic factors such as temperature and moisture, the composition of microbial communities and the plant functional groups present, suggest a high degree of context dependency of arthropods on aboveground-belowground processes (Eisenhauer et al., 2011; Scheu et al., 1999; Wall et al., 2008). The effects that arthropods have on microbes and ecosystem processes and the conditions that modulate them remains a rich area for further investigation (Yang and Gratton, 2014).

3d. Additional services

In addition to their direct effects on pest suppression, pollination and nutrient cycling, arthropods provide other benefits to people in agricultural landscapes. In the process of decomposing animal feces, arthropods can help suppress foodborne pathogens in organic vegetable production systems (Jones et al., 2015, 2019a) and reduce gastrointestinal parasites in animal-based systems (Sands and Wall, 2017). People use insect-derived products like honey, wax and silk, and insects themselves can be used as food for both domesticated livestock and directly for people (Schrader et al., 2016). Moreover, many inland fisheries depend on arthropod-based food webs, which include insects such as midges, mayflies and caddisflies (Dodds and Whiles, 2010; Losey and Vaughan, 2006; Vander Zanden et al., 2011). Recreational fishing of inland waters was estimated in 2018 at $42 billion in value (ecotourism, fishing licenses, equipment), with over 526,000 jobs supported (Allen et al., 2018). Similarly, insectivorous birds and bats are important for wildlife-watching based tourism, an industry that contributes annually over $13 billion to local economies and supports 660,000 jobs (Carver, 2013). This is a double win for people as bats' contribution to insect pest suppression in agricultural systems in North America is estimated at an additional $3.7 billion per year (Boyles et al., 2011).

Finally, the popularity of community science monitoring programs aimed at insects such as butterflies, bees and dragonflies (Crain et al., 2014; Oberhauser and LeBuhn, 2012) shows people enjoy spending time observing insects in nature. In North America, public and private parks based on overwintering roosts of monarch butterflies attract tens of thousands of tourists annually and contribute to local rural economies (Kido and Seidl, 2008). Together, these cultural and supporting arthropod services contribute to both people's material livelihoods as well as a greater sense of connectedness to nature (Breeze et al., 2015). Though we recognize the diverse ways in which arthropods can benefit people's lives (Schowalter et al., 2018), we limit the rest of this paper to those services that are most agriculturally relevant in North America and for which there is the most information available, especially pest control and pollination.

4. Ecological drivers of arthropod-based services

Many ecosystem services are determined by complex sets of ecological interactions. The factors that control them are studied at the intersection of applied fields, such as conservation biology and agroecology and the field of basic ecology which focuses on understanding ecological processes that govern species and their interactions. In this section we discuss how ecosystem function is influenced by the abundance and diversity of organisms, the resources upon which these organisms depend to carry out their life cycles and how populations of these organisms are influenced by spatial and temporal heterogeneity in agricultural landscapes (**Fig. 2** green boxes). We note that much of the evidence for how landscape structure affects service-providing organisms originates from outside North America, especially Europe.

4a. The critical role of biodiversity

Designing agricultural landscapes for arthropod services

An important pattern that has emerged in ecology in the last 30 years is the positive relationship between species diversity and ecosystem function (Cardinale et al., 2006; Hooper et al., 2005). The biodiversity-function relationship occurs across various ecosystem types, processes and trophic levels. While there are certainly exceptions, in general the relationship takes the form of a saturating curve; as the diversity of organisms increases, a given function in an ecosystem increases steeply at first then levels off. The biodiversity-function relationship applies to a wide range of ecosystem functions, often including the subset that we value as ecosystem services (Section 3). This means that in general, more diversity of service providers is thought to be better. Most tests of the biodiversity-function relationship have taken the form of manipulative experiments at small spatial scales in the lab and greenhouse (Cardinale et al., 2006, Hooper et al., 2005), but recent syntheses and meta-analyses of arthropod-based services support the idea that this relationship bears out in more complex systems at landscape scales. For example, levels of pollination and pest suppression in crop fields increase with diversity of pollinators and natural enemies, and respond more strongly to diversity than to abundance of these organisms (Dainese et al., 2019). Similarly, in a meta-analysis of 250 studies Letourneau et al. (2009) found that in over 70% of the studies increasing predator richness tended to increase herbivore suppression. A meta-analysis of decomposition studies also found strong positive effects of consumer species richness on organic matter depletion rates (Srivastava et al., 2009).

Why should we expect a positive relationship between diversity and function (or in our case, services)? First, as diversity increases, so do the chances that the species pool will include an organism that strongly contributes to the ecosystem service being measured (the “sampling” effect). Second, as diversity increases so do the chances that organisms will use resources or impact their environment in ways that are complementary or that facilitate one another. Both mechanisms contribute to the so-called “portfolio” effect, whereby having diversity ensures some level of insurance of function given spatial or temporal heterogeneity or disturbance to a system (Hooper et al., 2005).

Understanding the interactions between organisms in a food web context, however, can give more nuance and texture to biodiversity-function relationships in agroecosystems. For example, when predator diversity increases so does the possibility of intra-guild predation, in which predators attack each other leading to decreased control of herbivores (Rosenheim et al., 1995; Finke & Denno, 2004), though this effect is infrequent and weak (Janssen et al., 2006; Rosenheim and Harmon, 2006). In a study of dung beetle decomposition of animal feces, Wu et al. (2011) showed that in the presence of a dung beetle predator, feces consumption rates and nutrient release decreased, as did plant growth around dung pats, showing that top-down effects can also happen in “brown” food webs (Schmitz, 2010). Competition between invertebrate decomposers in soils can also result in lower than expected ecosystem responses such as nutrient cycling and plant growth, compared to instances when species are alone (Scheu et al., 1999). Management can encourage complementarity of species and minimize competition and intra-guild predation between these organisms (Snyder, 2019). Another source of complexity occurs when mutualisms disproportionately affect ecosystem structure and processes. For example, aphids and ants can form a ‘keystone mutualism’ in which ants change their foraging patterns in order to collect honeydew from aphids, transforming the arthropod community on crops because the ants so strongly affect the distribution of other organisms (Kaplan and Eubanks, 2005). In sum, these types of nuanced interactions between organisms suggest in some cases we need to understand the specific nature of interactions within communities rather than focusing on overall levels of biodiversity *per se*.

Designing agricultural landscapes for arthropod services

Finally, though we usually evaluate organisms' roles in an ecosystem in terms of their abundance or taxonomic diversity, it may be more useful to view them through the lens of functional traits. Functional traits are morphological, physiological, or phenological characteristics of species, and these can be better than taxonomy for predicting how organisms affect ecosystem processes (Cadotte et al., 2011; Wood et al., 2015). So far, links between trait diversity and ecosystem services have been explored in more detail with regards to plant diversity than arthropods (Díaz et al., 2007; Faucon et al., 2017). Much of the research on arthropod traits to date focuses on how trait diversity responds to field-scale management or landscape structure (Gámez-Virués et al., 2015), but some studies have begun to test how arthropod trait diversity predicts ecosystem service delivery. For example, in one study pollination of pumpkins increased with pollinator diversity, but the increase was better explained by diversity in bee functional groups than it was by species diversity (Hoehn et al., 2008). In another, diversity in functional traits did a better job than taxonomic diversity in predicting a range of ecosystem processes, including pollination and pest suppression (Gagic et al., 2015). Grab et al. (2019) were able to link landscape simplification to declines in pollinator phylogenetic diversity (correlated with functional diversity) and ultimately to reduced apple yield and quality, demonstrating both landscape filtering by species functional traits and consequent loss of ecosystem services.

In soil communities, functional diversity can be a more useful way to characterize species assemblages because of the high redundancy and similarity of species within these heterogeneous environments (Hättenschwiler et al., 2005). For example, Brousseau et al. (2019) found that variation in litter resource diversity explained the functional characteristics of arthropod decomposer communities, but not species composition. Functional diversity of dung beetles has also been shown to be necessary to provide multiple ecosystem services (dung removal, soil fauna activity and soil aeration) in pasture-based production systems (Manning et al., 2016).

In conclusion, several lines of evidence suggest ecosystem services are enhanced when there is a greater diversity of service providers. However, interactions between organisms, such as mutualisms and predation, can add considerable texture to this pattern. Finally, while we usually perceive biological diversity in taxonomic terms, organismal traits tend to have a closer connection than species diversity to ecosystem service delivery.

4b. Resources for service providers in agricultural landscapes

Leveraging ecosystem services from arthropods requires a knowledge of what taxa provide these services and what resources they need in their environment to be most effective. While the specifics vary depending on which services are most desired, the general approach can be informed by the applied science of Conservation Biological Control (CBC), where the focus is on enhancing the activity and effectiveness of existing natural enemies to provide pest suppression (Begg et al., 2017; Rusch et al., 2017). The CBC approach can be summed up simply as: 1) stop doing things that harm or restrict the effectiveness of service-providing organisms (e.g. unnecessary tillage, pesticide applications, or destruction of semi-natural habitats) and 2) start doing things to enhance service provider effectiveness (e.g. providing food, shelter and other necessary resources). A subset of CBC practices that focus on habitat management (Landis et al., 2000) are particularly relevant to designing agricultural landscapes.

Designing agricultural landscapes for arthropod services

Habitat management focuses on understanding resource requirements of service-providing organisms; for example, natural enemies needs for shelter, nectar, alternative prey/hosts and pollen (sometimes referred to as SNAP; Gurr et al., 2017). Service providers often require shelter from adverse conditions including locations for overwintering or aestivation, refuge from pesticides or unfavorable conditions within crop fields (e.g. dust, high temperatures; Gontijo, 2019; Griffiths et al., 2008). Refuges can be provided within or near crop fields to provide safe habitat and encourage recolonization of crop habitats. “Beetle banks”— narrow strips of tussock-forming grasses within crop fields—have been used in Europe to provide overwintering habitat and alternative food resources for ground-dwelling beetles promoting more rapid colonization of fields in the spring and improved control of pest aphids (Collins et al., 2002). In the US, similar habitats function to promote recolonization of adjacent insecticide treated crops by ground beetle communities (Lee et al., 2001) that prey on both insects (Menalled et al., 1999) and weed seeds (Menalled et al., 2001).

Nectar and pollen are essential food resources for pollinators and many natural enemies. Research evaluating the nutritional requirements of service-providing species and the attractiveness of different plant species and floral traits can be a valuable strategy for designing effective habitat management schemes. For example, little is known about the nutritional requirements of wild bee species, but linking macronutrient ratios in pollen collected by bees to those found in different flower species could inform better conservation practices (Vaudo et al., 2020, 2015). Natural enemies such as parasitoids frequently live longer and reproduce more effectively when they have regular access to floral resources (Wratten et al., 2003). These resources can be provided by exotic plants (Hickman and Wratten, 1996), but others have argued that the use of native plants to provide pollen and nectar is preferable (Isaacs et al., 2009, Tallamy 2007). This has led to efforts to screen native plants to select a set of species that in combination provide continuous floral resources, are attractive to pollinators and natural enemies, and which can survive under variable field conditions of full sun to shade, or wet to dry soils (Fiedler and Landis, 2007a, 2007b; Lundin et al., 2019, Howlett et al., this issue). Appropriate combinations of species have been planted adjacent to crop fields where they have been shown to increase spillover of natural enemies and pollinators and even increase yields (Blaauw and Isaacs, 2015, 2014). Similar research programs have focused on identifying and deploying plants as insectary hedgerows in California (Long et al., 2017; Morandin et al., 2014). A recent global meta-analysis on the effectiveness of similar practices concluded that flower strips, but not hedgerows, enhanced pest control services in adjacent fields but that effects on crop pollination and yield were more variable. Perennial flower strips with higher flowering plant diversity enhanced pollination more frequently but the effects drop off rapidly with distance to edge (Albrecht et al., 2020). Another meta-analysis reached similar conclusions, that adding floral resources to field margins increased the number and diversity of pollinators at the field edge but had inconsistent effects in field interiors (Zamorano et al. 2020). While these examples largely focus on field-scale enhancements, arthropods often move between habitats and collect diverse resources beyond the scale of a single crop field; therefore, resource needs should be considered at landscape-scales, such as in the selection of plant species for habitat restorations or the planting of complementary crop types in adjacent fields.

Assuring that the agricultural landscape also supports alternative prey for generalist natural enemies is a longstanding principle in CBC (Altieri and Letourneau, 1982; Harwood and Obrycki, 2005). Foundational studies in rice showed that abundant early season prey (mostly non-pest detritus feeders) were key to sustaining generalist predators that suppressed key pests later in the season (Settle et al., 1996) and similar effects occur in other crops (Landis and van der Werf, 1997). In models, alternative prey in field edges have been shown to allow for population build-up and easy spillover of natural enemies, which can then control key pests in adjacent crops (Bianchi and Werf, 2004). Conversely, the presence of alternative prey can in some cases decrease levels of pest suppression via competitive or lethal interactions between generalist predators (Koss and Snyder, 2005; Symondson et al., 2006).

In summary, part of designing agricultural landscapes for increased services entails identifying the resource needs of service providers and developing habitat management tools and techniques to provide those resources. They are more likely to be provided at sufficient levels when landscapes are heterogenous, as detailed in the following section.

4c. Spatial heterogeneity at landscape scales

Landscape structure is often described along two axes, composition and configuration. Composition refers to the amounts of different habitat types on the landscape. For example, the cover of different crops, forest, or grassland, or the overall diversity in habitat types that can be found represents what is present in a landscape. Configuration, on the other hand, refers specifically to the size, shape and spatial arrangement of individual habitat patches (Fahrig et al., 2011). Evidence suggests that increasing heterogeneity of both of these dimensions of landscape structure (**Fig. 4**) can enhance biodiversity and ecosystem services, and that their effects are often interactive (Martin et al., 2019; Sirami et al., 2019, Mitchell et al. 2015).

Compositional heterogeneity occurs when an agricultural landscape contains non-crop habitat **(Fig. 4b)** or a greater diversity of habitats, including crop types (**Fig. 4c**). Heterogeneous landscapes are hypothesized to enhance services like pest suppression and pollination because many natural enemies and pollinators require resources found in semi-natural habitats or benefit from variation that arises from management for many crop types instead of just one. Syntheses of studies on wild bees (Kennedy et al., 2013) and natural enemies (Chaplin-Kramer et al., 2011) have found their abundance and richness tend to be higher in crop fields surrounded by more high-quality and/or non-crop habitats. A global analysis of 89 crop systems and 1,475 locations was able to take this one step further, showing that farm fields in landscapes with more non-crop habitat have higher diversity of pollinators and natural enemies and higher rates of pest suppression and pollination (Dainese et al., 2019). This study suggests that while landscape structure moderates both the diversity and abundance of service providers, it is their diversity rather than abundance that translates into better service provision. This is particularly true for pest suppression: when we consider natural enemy abundance rather than diversity, effects of landscape composition are much less consistent (Dainese et al., 2019; Karp et al., 2018). Moreover, Sirami et al. (2019) found that in agricultural landscapes across Europe and Canada, the number of crop types and the heterogeneity of crops was more important in determining the amount of multi-trophic diversity in crop fields than the amount of surrounding natural areas. However, in some cases crop diversity has been documented to reduce the abundance of service providers, highlighting the relevance of crop identity and management and not just crop diversity *per se* (Hass et al., 2018).

The spatial arrangement of habitats in a landscape also affects service provision, with more complex configurations (**Fig. 4d**) generally thought to be desirable. There are a few hypotheses for why this should occur. First, beneficial organisms often spill over along boundaries between habitats (Blitzer et al., 2012; Rand et al., 2006), so it follows that visits or immigration events to crop fields from non-crop habitats can increase when the two cover types are intermixed. Second, some organisms benefit from ‘resource complementation’: they use resources from multiple habitat types and therefore can locate them more easily when habitat patches are small and/or intermixed with one another (Dunning et al., 1992). Finally, fine-grained landscapes made up of smaller fields and habitat patches can have more variation in management practices and timing from field to field, providing refuge for beneficial insects if, e.g., fields are tilled or sprayed at different times (Vasseur et al., 2013).

Large scale syntheses of how landscape configuration affects pollination and pest suppression have started to emerge. Data from 1,515 landscapes across Europe show that landscape configuration and composition interact to affect natural enemies, pests and pollinators (Martin et al., 2019). This analysis also shows the critical importance of life history traits in determining how arthropods are affected by landscape structure. For example, between natural enemies that overwinter outside of crop fields, flying insects responded positively to compositional and configurational heterogeneity, while those that dispersed passively on the wind were not significantly affected, and ground dispersers were affected by configuration more strongly than composition. A synthetic review of how landscape configuration affects pest suppression found all but 2 of the 33 studies reviewed identified significant effects of configuration, although their direction was variable (Haan et al., 2020). In general, fine-grained landscapes made up of smaller patches led to greater natural enemy density in crop fields. Dimensions of configuration having to do with connectivity were also important but context-dependent: natural enemies and pests can either increase or decrease with proximity to non-crop habitats. Finally, habitat patches range in shape from simple to complex, but there is not enough evidence to say whether this aspect of configuration has important effects on pest suppression (Haan et al., 2020). Spatial scale is also a key consideration for ecosystem services (Lindborg et al., 2017). In particular, how an organism responds to landscape structure will depend on various life history traits (Miguet et al., 2016) such as how far it can disperse (With and Crist, 1995). This suggests that landscape design should occur at spatial scales relevant to the service-providing species of interest.

In summary, while not all studies are consistent, evidence generally suggests that landscapes with diverse crop types, sufficiently high levels of non-crop vegetation and/or small crop fields are more biodiverse and have better service provision.

4d. Temporal heterogeneity within and across seasons

In addition to spatial heterogeneity, temporal heterogeneity in agricultural landscapes can affect biodiversity and ecosystem services. This type of heterogeneity occurs both within and between growing seasons, and can arise from underlying vegetation phenology as well as agricultural management practices (Cohen and Crowder, 2017). The temporal heterogeneity that arises from vegetation phenology is intrinsically linked to landscape spatial heterogeneity, since the types of habitats present and their spatial arrangement influence the timeline of resource availability for service providing organisms (**Fig. 4f and g**).

Within growing seasons, vegetation asynchrony may be important for ensuring continuous resource access for service-providing organisms (Schellhorn et al., 2015). For example, both managed (Dolezal et al., 2019) and wild bee species (Mallinger et al., 2016; Mandelik et al., 2012; Riedinger et al., 2014;

Rundlöf et al., 2014; Williams et al., 2012) have been shown to benefit from temporally complementary floral resources in different habitats over the course of a growing season. Conversely, greater cover of a mass flowering monocrop in the landscape has been shown to decrease the density of managed and wild pollinators, despite providing a greater total amount of floral resources (Holzschuh et al., 2016). Temporal heterogeneity may thus provide more continuous resource access, supporting larger, healthier populations of pollinators contributing to crop pollination services. Similar dynamics may be important for natural enemies and pest control, as predators and parasitoids track food and shelter resources in different habitats over time (Iuliano and Gratton, 2020). Within-season heterogeneity can also mediate the timing of natural enemy immigration to and emigration from crop fields and thus their effectiveness as biocontrol agents (Costamagna et al., 2015; Schellhorn et al., 2014). Furthermore, disturbances like pesticide application and crop harvest can disrupt beneficial insect populations, but their timing could be coordinated to ensure refugia in the landscape (Schellhorn et al., 2015, 2014).

Increasing attention has recently been paid to the effects of inter-annual crop diversity (i.e., crop rotation) at the landscape scale on crop pests and natural enemies, especially in Europe (Bertrand et al., 2016; Rusch et al., 2013; Schneider et al., 2015; Szalai et al., 2014). Such between-season temporal heterogeneity has not yet been investigated thoroughly enough to make generalizations, but effects are likely to be highly dependent on the life history traits of the pest and enemy species of interest. For example, while (Bertrand et al., 2016) found that total ground beetle abundance increased with temporal heterogeneity of crops in the landscape over a 5 year period, species evenness decreased and habitat generalists dominated. Effects of landscape-scale crop rotation on pollinators are even more scarcely investigated (Pufal et al., 2017), but one study from France showed that when a greater proportion of cereal fields in oilseed rape landscapes had at least 1 year of grassland in a 5 year rotation, wild bee abundance and species richness in field margins increased (Le Féon et al., 2013).

Although much less is known about the consequences of temporal heterogeneity compared to those of spatial heterogeneity for biodiversity services in agricultural landscapes, existing evidence suggests that temporal heterogeneity may offer service providers complementary resources within and across growing seasons, and that these benefits may be especially strong for generalist species able to take advantage of multiple habitat types.

5. Principles for ecological design of agricultural landscapes

In the previous section, we summarized recent ecological studies that show the importance of arthropod biodiversity for providing the ecosystem services on which farming depends and how spatial and temporal heterogeneity in agricultural landscapes influence arthropod abundance and diversity. Here, we use these core findings to develop a set of principles and key questions that can help guide the intentional design of agricultural landscapes to support arthropod-based ecosystem services (**Table 1**). These ecological principles are not meant to be exhaustive, but rather serve as a starting point to be modified in light of the local context and new scientific findings. Additionally, arthropod-based services are just one part of a larger portfolio of services that need to be considered when designing landscapes. We encourage other scientists to build on, refine, or amend these principles toward promoting these other services as well. In general, we expect landscape attributes that promote arthropod-based services to be multifunctional and to align with other ecosystem services as well (e.g., Schulte et al. 2017).

Landscape design is an inherently transdisciplinary process that involves understanding the diverse needs of stakeholders and integrating them with scientific knowledge about how landscape function can be modified to increase desired services (Barrett, 1992). Moreover, landscape-based approaches to resource management recognize that land use decisions influence a diversity of outcomes that transcend individual property boundaries and thus have impacts across communities (Arts et al., 2017). Ecological outcomes, including those that arise from arthropods, are only one of many important performance criteria that need to be evaluated in the design process. Accordingly, we have also identified several socially-informed principles and practices to guide planning and implementation of habitat manipulations in the landscape (**Table 2**). Like the ecological principles in **Table 1**, we view these as a starting point to be modified in the future.

A first step for engaging landscape design is to identify stakeholders, which typically include farmers, other rural residents and landowners, local government, businesses and educational institutions (Steingröver et al., 2010) that have a vested interest in what functionality these landscapes should provide (Campellone et al., 2018; Duru et al., 2015). A process of deliberation and discussions helps identify and understand the values that stakeholders collectively hold (agricultural production, food security, aesthetic beauty, recreation potential, etc.) and which services a landscape is already providing (Dale et al., 2018). Importantly, power discrepancies between stakeholders present a challenge for agricultural sustainability transitions (Hendrickson et al. 2018, Rossi et al. 2019). For example, farmers make on-the-ground land use decisions that shape landscapes, but most operate within the confines of economic realities set in place by corporate entities and policymakers (Jackson 2008). Power relationships between stakeholders can be highly complex, spanning levels of aggregation (e.g. individuals, organizations and sectors), scales (e.g. local to international) and domains (e.g. financial, cultural, or legal), and different stakeholders wield different types of power (Avelino & Wittmayer 2016, Rossi et al. 2019). Agricultural transitions typically require a reconfiguration of these relationships, which can be brought about through collaboration (e.g. Bui 2016) or conflict (e.g. Turner et al. 2020, Skrimizea et al., this issue).

Next, researchers and other educators can integrate this information with existing knowledge to develop tools to work with stakeholders to explore alternatives. Knowledge may come from various sources, including Indigenous communities and other holders of traditional ecological knowledge (TEK) as well as scientific institutions (Martin et al., 2010; Vandermeer and Perfecto, 2013). One common approach is to couple models of ecosystem services with Geographic Information Systems (GIS) to provide stakeholders with various scenarios or alternative futures for their consideration (Goldstein et al., 2012; Meehan et al., 2013; Nelson et al., 2009; Qiu et al., 2018; Santelmann et al., 2004). This process has been referred to as participatory design (Murgue et al., 2015) or collaborative geodesign (Slotterback et al., 2016). In some cases, 'scorecards' that help quantify landscape characteristics may be useful; for example, the Xerces Society for Invertebrate Conservation has developed habitat assessment forms for pollinators and natural enemies that quantify farm-scale and landscape-scale features and allow for comparisons between sites (Xerces Society, n.d.).

While landscape design processes are sometimes focused on maximizing a single key function (e.g., Davis et al., 2017, Groff et al., 2016), they are more often geared toward maximizing multiple desired ecosystem services (Jones et al., 2013, Manning et al. 2018) or developing win-win outcomes for the environment and economic development (de Groot et al., 2010; Qiu and Turner, 2013). Arthropods on their own are unlikely to drive redesign of agricultural landscapes, but can be an important component when combined with other stakeholder concerns. For example, (Steingröver et al., 2010) described a participatory process where increasing pest suppression was a central focus, but also overlapped with stakeholder desires for increasing wildlife habitat, water quality and maintaining a traditional rural landscape aesthetic. Increasing water quality while simultaneously maintaining or increasing biodiversity is a common theme in multiple landscape design processes (Asbjornsen et al., 2014; Cacho et al., 2018; Lind et al., 2019, Schulte et al. 2017). Inevitably such processes involve trade-offs (Howe et al., 2014) and maximizing short-term economic returns may be at odds with maintaining high biodiversity levels (Lark et al., 2020; Power, 2010; Raudsepp-Hearne et al., 2010). Moreover, cultural services or issues of equity are often hard to include or compare in the evaluation of multiple ecosystem services (Halpern et al., 2013). Various methods for examining ecosystem service trade-offs have been developed (Groot et al., 2018), including quantifying cultural services (van Berkel and Verburg, 2014) and identifying ecosystem services “bundles,” i.e., suites of services that are enhanced by similar design features (Raudsepp-Hearne et al., 2010). Ultimately, landscape design is an iterative process. As stakeholder needs change or other social and environmental developments alter the landscape, renewed planning will be needed.

6. Opportunities for putting design into practice

So far we have discussed the need for agricultural landscape design, examined ecological evidence for how landscape structure affects arthropod-based ecosystem services and proposed design principles based on this evidence. How does a society act on these principles and begin transforming landscapes? This question is massive in scale and other authors can provide a more complete picture of these factors than we can, but here we scratch the surface of this topic and point to some emerging drivers that could function as leverage points to design agricultural landscapes with biodiversity in mind (**Fig. 2**, yellow box)

6a. Crop diversity

Within heavily cropped landscapes, one way to increase compositional heterogeneity is to diversify the types of crops grown. Historical trends in crop diversity in the U.S. show a decrease over time; for example, according to USDA data the average number of crops per county in the Upper Midwest declined from 12 in the 1950s to just 6 in 2000, with an associated decline in several native bumble bee species (Hemberger et al., in review). Agricultural policies have a strong hand in either promoting or discouraging crop diversity. In the U.S. the quadrennial Farm Bill, the key piece of legislation dictating food and agriculture policy, has historically encouraged farmers to prioritize corn, soybean, cotton and wheat due to subsidies and crop insurance built around these crops. Since insurance policies are based on historical yields by county, farmers who wish to diversify what they grow can face barriers accessing crop insurance. However, the Farm Bill now also includes crop-neutral insurance, such as the Whole Farm Revenue Protection (WFRP) program, which allows farmers to diversify by providing a safety net for crop types beyond the three largest commodities. This program was introduced in 2014 and may offer opportunities to increase crop types within agricultural landscapes.

Emerging crop markets will also change agricultural landscapes and in some cases may diversify them. For example, in 2018 the US loosened restrictions on growing hemp, triggering a growing market for industrial hemp and setting this crop on a trend to increasingly figure into agricultural landscapes (Mark et al., 2020). There are also a variety of bioenergy feedstocks that could be adopted in coming years as part of efforts to shift from fossil fuels to renewable energy sources. These feedstocks could range from annual crops like corn and sorghum to herbaceous perennial grasses like switchgrass and *Miscanthus* and woody species like poplar and pine. While turning to corn as a bioenergy feedstock exacerbates landscape simplification and further erodes ecosystem services (Landis et al., 2008), perennial crops tend to be more friendly to biodiversity (Núñez-Regueiro et al., 2020; Werling et al., 2014). Replacing annual crops with perennial bioenergy grasslands could strongly enhance ecosystem services (Landis et al., 2018; Robertson et al., 2017; Werling et al., 2014).

6b. Grower and consumer diversity

Changing demographics in the United States will also alter farming communities and those who utilize their outputs. Currently 95% of producers in the U.S. are white and 64% are men, in part because legacies of colonialism, slavery and institutionalized racism and sexism have enabled only a narrow segment of the population to have the legal standing and access to capital necessary to farm at commercial scales (Horst and Marion, 2019; Kelly et al., 2020). Accordingly, this has limited what modern agricultural landscapes look like. The current cohort of farmers is also aging, with nearly two thirds now over 55 (USDA NASS, 2019). Meanwhile, although systematic research is lacking, newer farmers appear to favor diversifying crops and trying new management practices (Ackoff et al., 2017; Baumgart-Getz et al., 2012; Prokopy et al., 2008). Programs that decrease barriers to starting farmers can help catalyze this change. For example, the 2018 Farm Bill established the Farming Opportunities Training and Outreach program, which includes initiatives aimed at socially disadvantaged and new farmers. Such initiatives may indirectly result in more heterogeneous, biodiversity-accommodating landscapes if newer farmers move beyond status quo conventional cropping systems. In addition, recent years have seen rapid growth in sales of USDA certified organic food to a $50 billion industry (Hellerstein et al., 2019), expanding interest in “local” food (e.g. farmers markets and community supported agriculture); (Low et al., 2015) and heightened concern for the conservation of insect pollinators (Sumner et al., 2018; Wilson et al., 2017). If these trends are any indication, consumer demand for products that are perceived as being tied to better social and environmental outcomes will increase in the future. These shifting consumer demands may also create opportunities for agricultural approaches that diversify crops and landscapes to the benefit of arthropod service providers.

6c. Conservation programs

Conservation programs are necessary to protect existing natural habitats and other uncultivated areas and to provide incentives for establishing new ones. Some U.S. Farm Bill programs, such as the Conservation Stewardship Program (CSP) and Environmental Quality Incentives Program (EQIP), support conservation practices on actively farmed land, while others like the Conservation Reserve Program (CRP) pay farmers to take cropland out of production for 10 or more years and plant grassland, pollinator strips, or buffer strips instead. The landscape features incentivized by these programs can provide resources to service providers and enhance spatial heterogeneity in addition to improving soil conservation and limiting nutrient loss. Unfortunately, conservation programs are at odds with other parts of the Farm Bill—such as crop insurance subsidies—that incentivize the cultivation of a limited set of intensively managed crops. Furthermore, the amount of land enrolled in CRP has been declining steadily for over a decade, from a peak of over 35 million acres in 2007 to fewer than 24 million in 2018 (Bigelow et al., 2020). Conservation programs could make a stronger impact on landscape structure if they were funded more aggressively and buffered from market forces that push farmers to convert them back to crops. While plantings occur at the field or farm scale, incentives could be designed specifically to catalyze change at larger spatial scales. For example, landscape-scale coordination could be encouraged by offering payments that compound when neighboring farms adopt complementary practices (Goldman et al., 2007; Lefebvre et al., 2015). These types of “agglomeration bonuses” have been explored to enhance pollinator habitat conservation in a Wyoming landscape (Panchalingam et al., 2019). The same principle could be used to encourage neighboring farmers to coordinate similar initiatives and produce landscapes that are richer in resources for service-providing organisms.

6d. Technology-based opportunities

Technological development has historically been an important catalyst of landscape simplification in North America (section 2). However, if used appropriately, new technologies could help us reimagine farming in ways that increase landscape heterogeneity and facilitate promising conservation practices (Basso and Antle, 2020). Precision agriculture is the use of technologies to manage spatial and temporal variability in agriculture (Pierce and Nowak, 1999). Many farmers now use high-resolution yield monitoring which can help them maximize profits by identifying where fertilizer inputs are most effectively used. Importantly, this technology can also reveal areas within crop fields which underperform. Using 2015 prices, Brandes et al., 2016 found that as much as 27% of Iowa, USA cropland was losing more than $250/ha. Basso et al. (2019) used a combination of remote-sensing and crop modeling, validated with high-resolution yield monitoring, to show that corn and soybean fields in the Midwest US contain areas of consistently high, low or fluctuating productivity. Their analysis shows that stable low-productivity portions of fields comprise 28% of the cropland in this region and disproportionately contribute to nitrogen pollution. This improved understanding of where high and low yielding areas occur within farm fields creates the opportunity for precision conservation, defined as the use of precision agriculture approaches to achieve conservation goals (McConnell and Burger, 2018). Farmers can increase profits by strategically taking subsets of fields out of production, making these areas available for other conservation objectives. So far, adoption of precision agriculture and precision conservation has been modest (Barnes et al., 2018; McConnell, 2019; Schimmelpfennig and Ebel, 2016). Nevertheless, if precision techniques continue to be adopted as generational turnover in farmers occurs, impacts on landscape structure could be beneficial.

Looking further to the future, in coming decades farming in North America is likely to become increasingly automated. Unmanned aerial vehicles (i.e., drones) are increasingly used for monitoring in precision agriculture (Radoglou-Grammatikis et al., 2020). There are also a growing variety of robotic systems for weeding, harvesting and applying chemicals (Roldán, 2018) which have not been widely adopted but could become mainstream as technologies mature and if agricultural labor shortages increase. Tractors are increasingly equipped with guidance and other technologies to reduce reliance on human operators and fully autonomous tractors are expected to become available (Thomasson et al., 2019). We can only speculate about how these new tools may affect landscape structure. However, up to this point in time, tractor design and resulting field configurations have been centered around a human operator, with a key consideration of how much ground can be covered during a workday. This has in part driven the trend toward larger machinery and simple, consolidated fields (MacDonald et al., 2013). Without a human operator it may become more economical to deploy smaller tractors for longer amounts of time or multiple devices working in parallel (i.e., “robot swarms”), meaning smaller fields with complex shapes would be more feasible to farm (Lowenberg-DeBoer et al., 2019). However, concerns remain about how various digital farming technologies may concentrate power, exacerbate corporate dependence at the expense of farmer autonomy and create technological lock-ins to an industrial model of agriculture (Clapp and Ruder, 2020).

6e. Climate change

Future changes to landscape structure will occur in the context of climate change. Shifts in temperature and precipitation will dictate in which regions crops can be grown. In general, agricultural climate zones are expected to shift northward (King et al., 2018) and production of staple grain crops in the United States is expected to shift north and east (Cho and McCarl, 2017). Farmers will modify the crops they grow, probably resulting in new rotation schemes (Bohan et al., this issue). We should also expect changes in wild biodiversity, including the service-providing species on which we depend (Kjøhl et al., 2011; Soroye et al., 2020; Thomson et al., 2010). Maintaining high levels of biodiversity will be important for buffering against changes in the ranges or phenologies of service-providing organisms. For example, Bartomeus et al., 2013 show that the diversity of the wild bee community in apple orchards can ensure synchrony between the timing of apple bloom and pollinator activity periods.

“Climate smart agriculture” has emerged as a framework for developing farming systems that are resilient to climate-induced shocks (i.e., adaptation) as well as reduce greenhouse gas emissions and sequester carbon (i.e., mitigation). Scherr et al. (2012) propose “climate smart landscapes” to move beyond farm-scale practices and consider how diverse land uses may interact to dilute risk and leverage multiple co-benefits for agricultural production, biodiversity and climate. Many of the practices they highlight for climate mitigation and adaptation, such as increasing perennials on the landscape, maintaining undisturbed natural vegetation and restoring degraded habitat (Scherr et al., 2012), are also likely to benefit arthropod service providers.

7. Conclusions

We have synthesized research on the relationship between landscape structure and beneficial arthropod populations into a set of principles for guiding agricultural landscape design. Although patterns relating landscape structure and arthropod-based ecosystem services are variable and highly context-dependent, the latest evidence suggests that diverse, complex landscapes can best support communities of ecosystem service providers. Emerging questions from recent literature highlight the importance of species functional traits, landscape configuration and temporal dynamics.

- Accounting for the functional traits of pollinators, natural enemies and pests seems to substantially improve predictions about how changes in landscape structure will affect species distributions (Martin et al., 2019; Wood et al., 2015). Thus, agricultural landscape design may be most successful when tailored to particular traits of high-priority species or groups.
- Recent syntheses show landscape configuration can have strong effects on service providers, but these are hard to generalize and less well studied than composition effects (Haan et al., 2020). This is important because the arrangement of habitats in space is especially relevant to service delivery (and not merely the conservation of beneficial species), as it filters how and when organisms move to crop fields where they are needed.
- Finally, patterns of crop phenology, service provider activity and their use of resources over extended periods of time have only recently garnered attention from researchers. By experimentally clarifying these patterns in particular agricultural contexts, we may be able to develop more targeted, mechanistic design interventions than are currently possible from simple correlations with landscape structure (Iuliano and Gratton, 2020; Pufal et al., 2017; Schellhorn et al., 2015).

Much of the research discussed above, especially studies investigating crop diversity and configuration effects on arthropod service providers, originates from Europe. This may reflect the fact that in Europe landscape ecology is an older discipline that developed with a more normative bent toward managing landscapes with long histories of traditional farming (Naveh and Lieberman, 1994). In contrast, landscape ecology did not take off in North America until the 1980s, with more focus on describing spatial pattern as cause and consequence of ecological processes in “natural” systems (Turner, 2005). Although there is much to learn by deriving general principles from European examples, agricultural landscape design in North America could benefit from more local case studies and large-scale syntheses. Land managers and researchers have the opportunity to partner to produce context-specific, place-based research for landscape design that effectively achieves ecosystem service goals.

More work is also needed at the interface between biodiversity conservation and landscape design for ecosystem services (**Box 2**). Rare species may not contribute strongly to ecosystem services (Kleijn et al. 2015) and actions geared toward conservation and ecosystem service provision are often compatible but do not always complement one another reciprocally (Macfadyen et al. 2012). For example, agricultural landscapes with complex configurations can have enhanced ecosystem services within crop fields, but are they more or less effective for conserving rare species or biodiversity on the whole? Future work should continue to identify areas of complementarity and/or conflict in order to conserve biodiversity to the greatest extent possible while also building sustainable farming systems that benefit from biodiversity rather than external inputs whenever possible.

Despite the value of landscape heterogeneity for ecosystem services, many farming regions in North America are becoming increasingly homogenous. Productivist philosophies of agriculture, supported by economic systems that favor efficiency and globalization, continue to reduce the number of farmers and farms in our landscapes (Thompson, 2017; Wilson and Burton, 2015). Moreover, as human populations continue to move to cities (United Nations, 2019), a diversity of ideas, institutions and approaches to farming are lost from rural landscapes. These changes are mirrored in the loss of landscape heterogeneity that we highlight as being key to supporting the nature that ultimately underpins agriculture. To reconcile this discrepancy, communities must develop and leverage policy at the local and national levels to promote the active design of agricultural landscapes in order to achieve particular agroecological goals, rather than merely responding to exogenous drivers of change. By pairing ecological understanding with stakeholder values, communities can design landscapes that facilitate more sustainable agricultural systems that balance agricultural production, biodiversity conservation and human wellbeing (Arts et al., 2017). Ultimately, achieving ecosystem service goals will require an intentional and deliberate process of design, supported by the best available science, that enables communities to collectively chart a path towards multifunctional landscapes (Duru et al., 2015; Hölting et al., 2020) that supports not only arthropod biodiversity, but human well-being more broadly (Chaplin-Kramer et al., 2019).

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Designing agricultural landscapes for arthropod services

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Tables

Table 1. Key ecological principles and guiding questions for use in landscape design to enhance arthropod-mediated ecosystem services.

Principle	Key references	Guiding questions	Example case studies
Identify relevant service providers, their interactions and resource requirements	Gurr et al., 2017; Isaacs et al., 2009; Landis et al., 2000; Rader et al., 2016; Snyder, 2019; Vaudo et al., 2015	Which species pollinate flowers, consume crop pests and decompose waste?	Furlong, 2015; Gill and O'Neal, 2015; Jones et al., 2019b; Lee et al., 2019; Rutledge et al., 2004; Winfree et al., 2008
		How can resources be identified and manipulated to enhance beneficial species populations?	Fiedler and Landis, 2007a, 2007b; Gibson et al., 2019; Lundin et al., 2019; Rowe et al., 2020; Vaudo et al., 2020
Promote compositional heterogeneity	Chaplin-Kramer et al., 2011; Dainese et al., 2019; Kennedy et al., 2013; Sirami et al., 2019; Vasseur et al., 2013	How much off-field, natural, or semi- natural habitat is present?	Gardiner et al., 2009a, 2009b; Klein et al., 2012; Kremen et al., 2002; Perez-Alvarez et al., 2019
		How many different types of crops are grown?	Aguilera et al., 2020; Redlich et al., 2018; Riedinger et al., 2014
Promote configurational heterogeneity	Garibaldi et al., 2011; Haan et al., 2020; Martin et al., 2019; Sirami et al., 2019; Vasseur et al., 2013	What is the typical field size?	Elliott et al., 2002; Isaacs and Kirk, 2010; Martin et al., 2016
		How far are crop fields from adjacent habitat patches?	Bailey et al., 2010; Farwig et al., 2009; Schüepp et al., 2014

Manage spatial and temporal connectivity	Cohen and Crowder, 2017; Iuliano and Gratton, 2020; O'Rourke and Petersen, 2017; Schellhorn et al., 2015, 2014	Are the multiple resources required throughout the life cycles of service providing species present in close proximity?	Aviron et al., 2018; Koh et al., 2013; Mallinger et al., 2016
		When are there periods of resource scarcity or other management disturbances?	Macfadyen et al., 2015; Pope and Jha, 2017; Timberlake et al., 2019
		Can the resources that disservice-providing organisms (i.e. pests) rely upon be interrupted in space and/or time?	Parry et al., 2019; Schneider et al., 2015
Operate at relevant spatial and temporal scales	Haan et al., 2020; Lindborg et al., 2017; Miguet et al., 2016	How far do relevant service providers disperse or forage?	Rao and Strange, 2012; Sivakoff et al., 2012
		At what times of the year and for what duration are service providers most active?	Frank et al., 2008; Russo et al., 2013

Table 2. Key social principles and guiding questions for use in landscape design to enhance arthropod-mediated ecosystem services.

Principle	Key references & case studies	Guiding Questions
Assess stakeholder needs and wants for the landscape	Campellone et al., 2018; Duru et al., 2015; Matson et al., 2016; Slotterback et al., 2016; Steingröver et al., 2010	What are the values underlying stakeholder desires?
		Are diverse stakeholders included and are they represented equitably?
		Which services is the landscape already able to provide and which are lacking?
Explore and evaluate alternative landscape futures	Goldstein et al., 2012; Meehan et al., 2013; Nelson et al., 2009; Qiu et al., 2018; Santelmann et al., 2004	What are the range of possible future land cover and land use scenarios?
		Based on empirical data and landscape models, how can we expect service levels to differ across scenarios?
Recognize bundles and tradeoffs	Raudsepp-Hearne et al. 2010; Jones et al. 2013; Meehan et al. 2013; Howe et al. 2014	Which services and providers are likely to exhibit co-benefits from a given design intervention?
		How can stakeholder values inform management decisions in cases where multiple services are incompatible?
Anticipate and respond to drivers of landscape change as design barriers or opportunities	Basso and Antle, 2020; Radeloff et al., 2012; Sautier et al., 2017; Scherr et al., 2012	What technological, economic, or policy changes are likely to affect land cover and land use in the region?
		How can land managers influence and respond to drivers to reflect biodiversity-centric design principles?

Figures

Box 1. What are arthropod-based ecosystem services? All images under Creative Commons license.

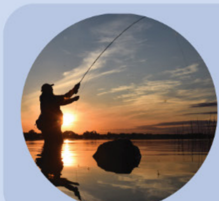
Box 1 What are arthropod-based ecosystem services?

Ecosystem services (ES) are the benefits that people derive from the rest of nature. The ES concept seeks to draw attention to how human wellbeing depends on non-human organisms and the broader environment, sometimes in ways that are not always immediately apparent. While this dependence has been recognized in principle from the earliest civilizations, ES emerged as a more formalized concept in the late 1970s and rose to prominence in the 1990s and early 2000s (Daily 2012, Gómez-Baggethun et al. 2010). In particular the United Nations' Millennium Ecosystem Assessment (MEA, 2005) was instrumental in formalizing and popularizing the concept, denoting four categories of services:

Regulating services create and maintain favorable conditions for human flourishing, such as liveable climate and healthy air quality. Two of the most prominent and best understood arthropod-provided services, pollination and pest suppression, are typically categorized here.

Supporting services are the foundational conditions upon which all other services depend. They include large scale, long-term processes such as soil formation, oxygen generation, and habitat provisioning. Arthropods are not the dominant group that provide these services, but taxa such as mites, springtails, and dung beetles help form soil and recycle nutrients.

Provisioning services are those that contribute directly and materially to products used by humans, such as food, timber, and water. While arthropods contribute to production indirectly via regulating services, they also generate products like honey and silk, or can be directly used for livestock feed or human consumption.



Cultural services are the non-material benefits that people derive from the natural world, such as recreation, aesthetic beauty, and spiritual experience. For example, the fishing and birding industries rely on insect-based food webs, and people enjoy viewing and collecting charasmatic arthropods like butterflies

Since its introduction the ES concept has been the subject of considerable contestation and debate, as definition, valuation, and incorporation of services into economic markets has been challenging (Dempsey & Robertson 2012, McElwee 2017, Schröter et al. 2014). Since the MEA, The UN—through the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)—has shifted from the ES concept in favor of "***nature's contributions to people***" to better capture the diverse worldviews, knowledge systems, and values that are brought to bear on human-nature relations (Dias 2018, Kadyaklo et al. 2019). Throughout this chapter we maintain the ecosystem services terminology, as we expect that it is more familiar to readers in the North American context.

Box 2. The relationship between biodiversity conservation and design for ecosystem services.

Box 2 The relationship between biodiversity conservation and design for ecosystem services

A central question that has emerged in landscape research is how to balance conservation objectives with the need for agricultural production. These goals are both critically important, but compete for the same limiting resource—land (Power 2010; Fischer et al. 2014; Arts et al. 2017). One long- standing debate has framed solutions for biodiversity conservation as a dichotomy between "land-sparing" and "land-sharing."

The **land-sparing** perspective advocates for concentrating agricultural productivity on select land in order to save other lands for conservation. At its extreme, it can be seen as advocating for intensified practices as a way to maximize yield within a smaller, if sacrificial, land footprint.

On the other hand, **land-sharing** focuses on using biodiversity-friendly agricultural practices and integrating semi-natural habitats with agriculture as a way to meet both sets of goals together (Green et al. 2005; Fischer et al. 2008). This view is, at its extreme, characterized as advocating for extensive agricultural practices that universally and invariably degrade natural habitats and leave fewer of them intact.

The land-sharing vs. land-sparing dichotomy has eroded somewhat in recent years. First, its framing is too narrow, detracting from the more fundamental question of how to secure human wellbeing in agricultural landscapes (Bennett 2017). Research has found that aspects of both approaches are useful in different contexts (Grau et al. 2013; Gilroy et al. 2014; Fischer et al. 2014; Grass et al. 2019). Additionally, there is increasing awareness that agriculture and biodiversity are deeply interdependent. Conservation has historically been dominated by a binary framework in which natural habitat patches were viewed as being surrounded by a hostile 'matrix' of agriculture (i.e., not habitat), but this is increasingly understood as simplistic (Perfecto and Vandermeer 2007). Making cultivated areas and field margins more hospitable to biodiversity is an important way to enhance connectivity among habitat patches, facilitate dispersal, and promote population persistence (Vandermeer and Perfecto, 2010). Agriculture is also dependent on diverse species for ecosystem services, which in turn depend on landscapes that harbor biodiversity across multiple spatial scales. ***Generally, what is emerging in place of the sparing vs. sharing debate is the principle that agricultural productivity and biodiversity conservation are intertwined, and that well-connected reserves, parks, and marginal set-asides are essential components of resilient, multifunctional landscapes*** (Kremen and Merenlender 2018).

There are still some instances in which landscape design for biodiversity conservation and for ecosystem services are incongruent, or where positive outcomes for one goal are neutral or negative for the other (Macfadyen et al. 2012). Some services are rendered by very common taxa that are not typically of conservation concern (Kleijn et al. 2015) . Others are performed by exotic species; for example, the ladybeetle community that helps suppress soybean aphids is increasingly made up of exotic taxa (Bahlai et al., 2015), and managed European honeybees are often important crop pollinators (Brittain et al., 2013). Macfadyen et al. (2012) argue that while efforts intended to conserve biodiversity in agricultural landscapes often have positive effects on ecosystem services, the reverse is not always true.

Progress is being made to narrow the perceived gaps between biodiversity conservation goals and ecosystem services and to maximize their complementarity. For example, recent syntheses have found that diversity of pollinators and natural enemies, more than abundance, enhances services (Dainese et al., 2019). This suggests complementarity between the two objectives, although in some cases the diversity required for maximum ecosystem service provision is lower than goals set for conservation (Macfadyen et al., 2012). Appropriate strategies will depend on local context, such as levels of biodiversity and the landscapes and crop types being considered (Cunningham et al., 2013). In contexts where stakes are high for conservation, landscape design should be geared more directly toward this goal, while in other cases, such as in landscapes already dominated by agriculture, design efforts could prioritize ecosystem service provision which will likely result in some conservation benefits as well.

Figure 1. Processes in a crop field are influenced by the surrounding landscape. Within a field (black lines and arrows), organisms are influenced by field-scale practices like tillage and cover cropping (reviewed elsewhere), and organisms are also exchanged between the field interior and the field edge where small amounts of unmanaged vegetation or intentionally-planted perennial strips can occur. At the farm scale (white lines and arrows), service-providing organisms spillover across boundaries between crops, patches of grassland and woodlots that may comprise an individual farm. Finally, at the landscape scale, many organisms disperse longer distances and may originate from, or use resources in, habitat patches that are located hundreds or even thousands of meters from a crop field (blue arrows). Image under Creative Commons license.

Designing agricultural landscapes for arthropod services

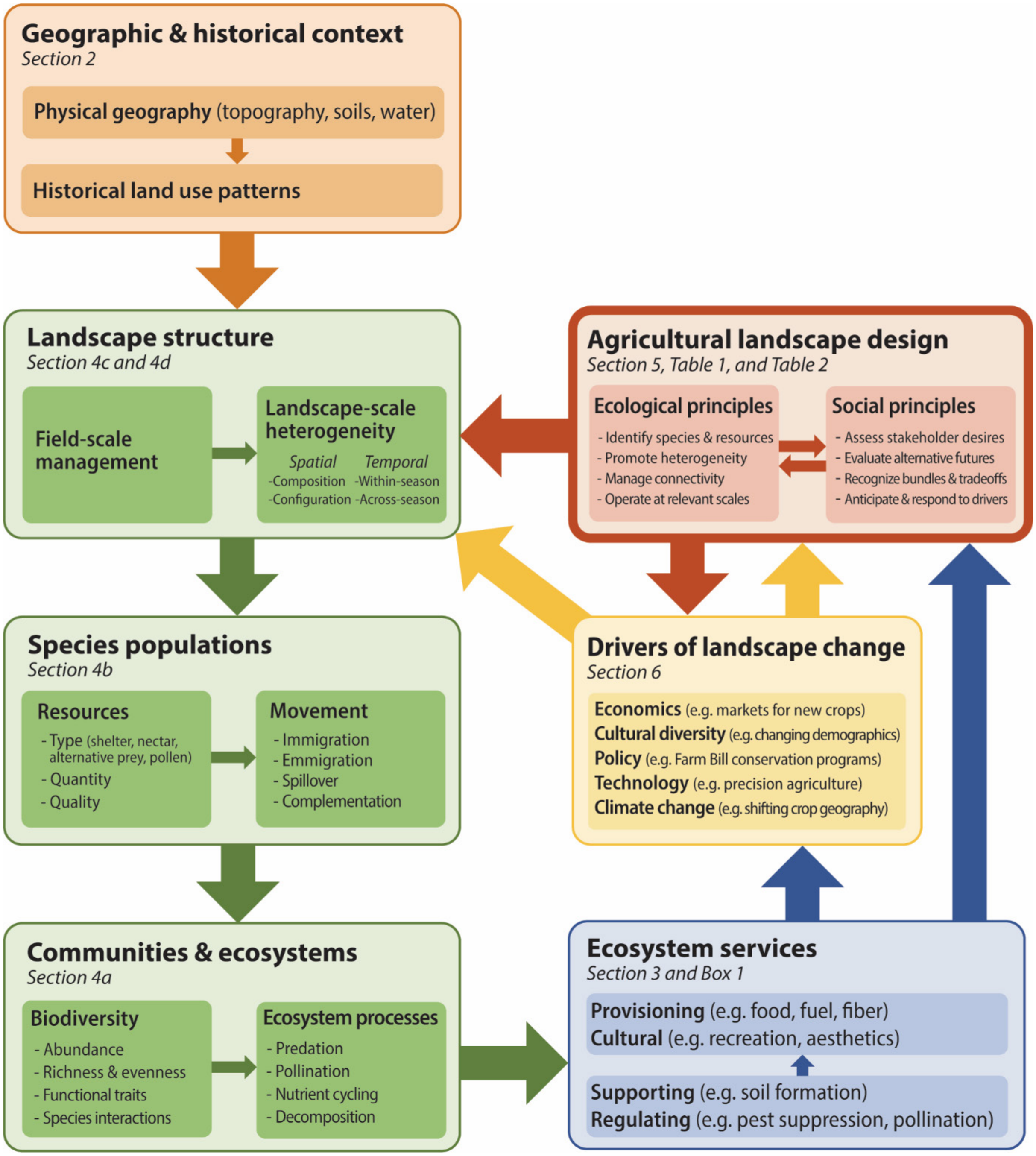


Figure 2. Summary diagram depicting the relationships between landscape design, ecological drivers of arthropod service providers and biodiversity services to agriculture. Different colors correspond to different article sections, which describe box contents in greater detail.

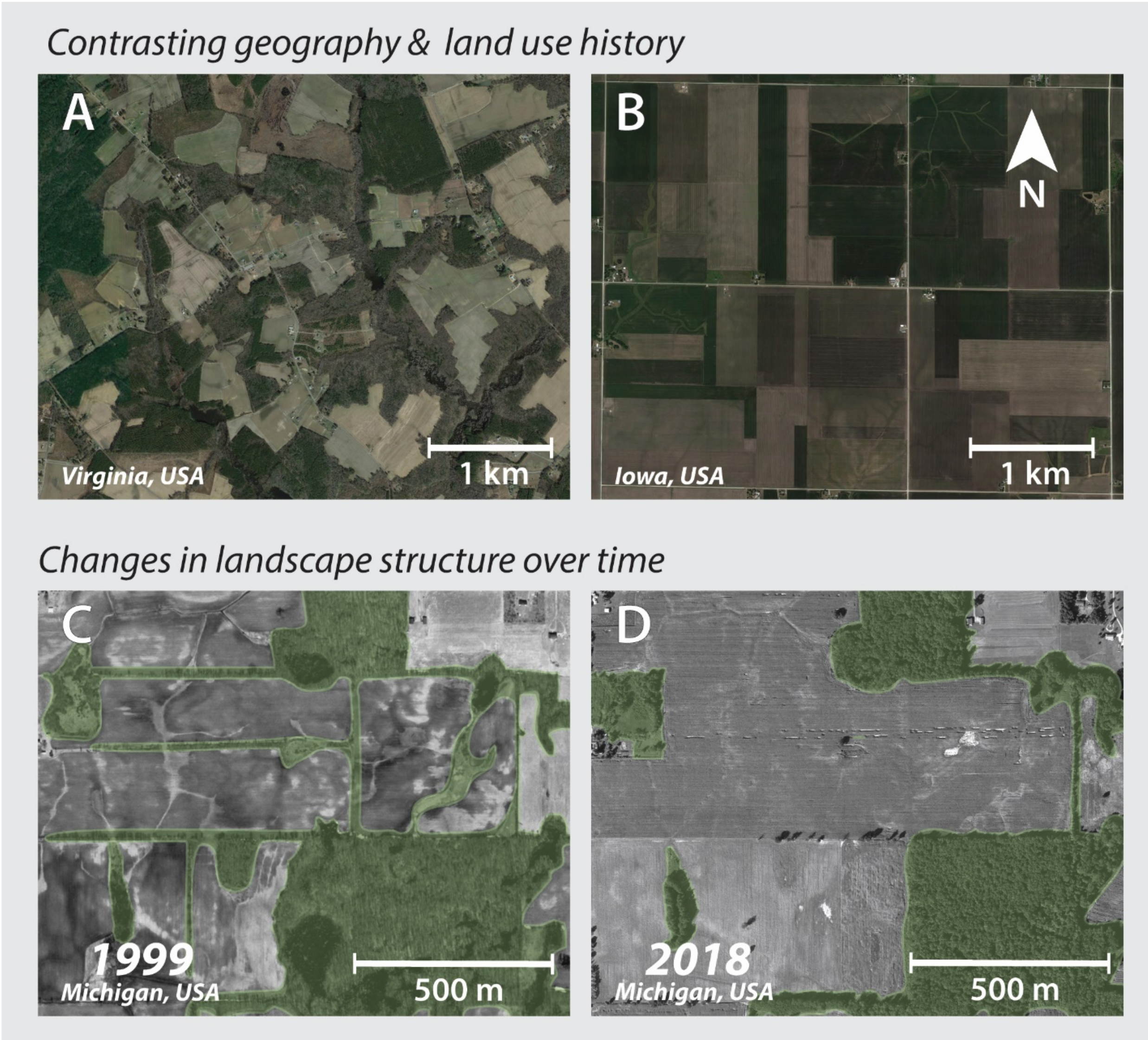


Figure 3. Contrasting North American agricultural landscapes in **A**) Southeastern Virginia, US and **B**) Southeastern Iowa, US. Differences in initial land survey systems contribute to the distinct landscape structures seen here. Panels **C** and **D** show an example of how removing hedgerows and other uncultivated habitat patches (shaded in green) around crop fields in Michigan, USA has led to landscape simplification.

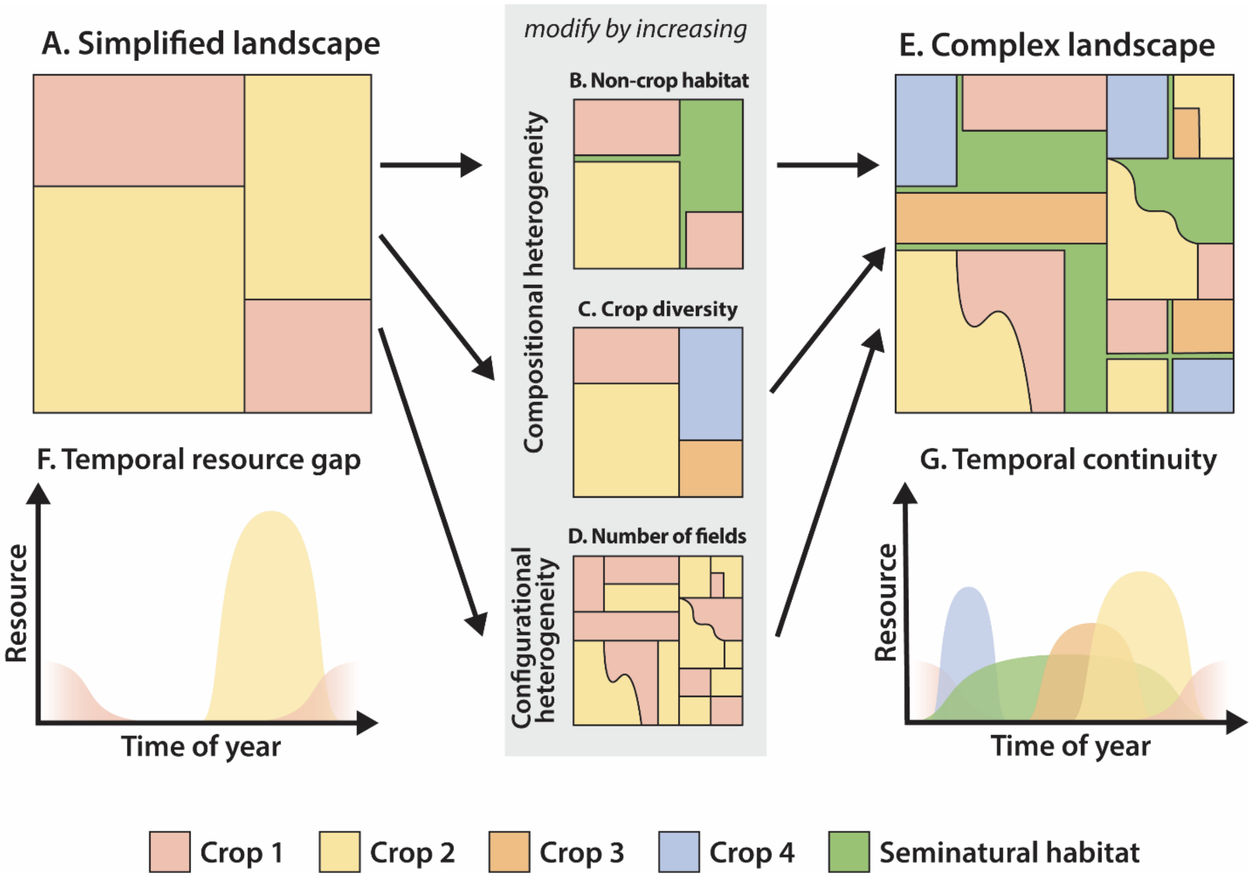


Figure 4. Conceptual representation of multiple dimensions of agricultural landscape heterogeneity. **A**) depicts a simplified landscape with only two crop types. This landscape can be made more complex by increasing the compositional heterogeneity via **B**) addition of non-crop habitat patches (or preservation where they already exist), or **C**) diversification of crop types planted. Configurational heterogeneity can be increased by **D**) breaking up large fields into smaller ones, creating more edges between different land cover types. These distinct spatial modifications can be implemented in combination to create **E**) a highly complex landscape. Depending on their phenologies, different combinations of landcover types produce temporal heterogeneity on the landscape, which may result in **F**) resource gaps or **G**) resource continuity throughout the life cycles of service-providing species.