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Hedgerows as Ecosystems: Service Delivery, Management, and Restoration

Ian Montgomery,[1] Tancredi Caruso,[2] and Neil Reid[1]

[1]Institute of Global Food Security, School of Biological Sciences, Queen's University of Belfast, Belfast BT9 5DL, Northern Ireland, United Kingdom; email: i.montgomery@qub.ac.uk, Neil.Reid@qub.ac.uk

[2]School of Biology and Environmental Science, University College Dublin, Dublin 4, Ireland; email: tancredi.caruso@ucd.ie

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Abstract

Hedge density, structure, and function vary with primary production and slope gradient and are subject to other diverse factors. Hedgerows are emerging ecosystems with both above- and belowground components. Functions of hedges can be categorized as provisioning, regulating, cultural, and supporting ecosystem services; these functions include food production, noncrop food and wood production, firewood production, pollination, pest control, soil conservation and quality improvement, mitigation of water flux and availability, carbon sequestration, landscape connectivity and character maintenance, and contributions to biodiversity. Urban hedges provide a relatively equitable microclimate and critical connections between green spaces and enhance human health and well-being through contact with biodiversity. Soil and water conservation are well researched in tropical hedges but less is known about their contribution to pollination, pest control, and biodiversity. Establishing a minimum hedge width and longer intervals between cutting of temperate hedges would enhance biosecurity and promote carbon sequestration and biodiversity. Hedges have a global role in mitigating biodiversity loss and climate change, which restoration should maximize, notwithstanding regional character.

INTRODUCTION

Hedges protect crops and livestock and mark boundaries while also providing fuel, timber, and food. They have a critical role in the landscape and ecology of farmland and are essential to food and water provision and quality (Baudry et al. 2000). The contribution of hedgerows to conservation of biological diversity (Arnaiz-Schmitz et al. 2018) is compromised by agricultural intensification (Boutin et al. 2011). Decreased hedgerow length reduces landscape connectivity and disrupts the spatial ecology of populations and communities (Burel 1992). However, hedges remain important contributors to biodiversity: In northwest Europe, a recent survey across farm types indicated that hedges were present on 100% of farms, providing linear habitats comprising 10% of total land area and 43% of wildlife habitat (Larkin et al. 2019).

Government responses to loss of hedgerows and consequent changes in biodiversity, through agri-environmental schemes (AESs), aim to maintain or restore hedge length or buffer strips. We review the evidence for the diverse roles of hedgerows and related features in agricultural systems and examine the impact of negative management; removal of mature hedges; and conflicts, real or imagined, between agriculture and conservation. While there are early studies on the direct effects of hedges on agricultural production, recent interests focus on pollination, pest control, and conservation of biodiversity and soil. There is also growing interest in urban hedges, which have less to do with production but act as a refuge for nature in cities and are therefore increasingly important for the 55% of humankind who live there.

Hedge refers to the woody plants that form a hedgerow, which also includes other plant species and features, but these terms are used synonymously (Dover 2019). It is difficult to classify hedges (Pollard et al. 1974). The only consistent hedge feature is its linear structure that is elevated above the surrounding ground level. Its lower levels are characterized by adjacent land use. Hedges are frequently composed of native plant species but may also be made up entirely of exotic, invasive plant species or simply stones. Hedges and their associated features—e.g., banks, ditches, verges, and trees—have similar or complementary functions. We define hedges broadly, presenting a general model of hedge structure and function. We describe ecosystem services (ESs) and the role of hedge management and restoration in their delivery and discuss the potential role of hedges in mitigating major environmental problems.

GLOBAL VARIATION

European hedgerows were constructed initially during deforestation around Neolithic settlements to protect livestock and crops. The field pattern delineated by low stone walls at Céide Fields in the west of Ireland dates from 3,500 BC, and Bronze Age Celtic fields have been found dating from 1,500 BC onward across northern Europe. Farmland in Britain, having been cleared of woodland, gradually became more enclosed with the development of hedges during the Iron Age and the Roman, Saxon, and early medieval periods, with a further 320,000 km of hedge being added after the Enclosure Acts were passed, from 1760 to 1820 AD. Increased mechanization required larger land parcels to maximize yields and profitability, leading to the loss of many hedges. Hedgerows have greater plant species richness than forest in Belgium, but 30% of hedges have been lost over the past 41 years (Van den Berge et al. 2019). The fastest rate of hedgerow removal in eastern England was 5,600 km/year in the 1960s (Pollard et al. 1974), with a cumulative loss of 27% (Dover 2019). Political and economic systems also impact hedges; for example, much of Czechoslovakia lost scattered vegetation during the period when the collective farm system was active. More recently, land managers seeking to restore landscape features, particularly owners with larger holdings close to urban areas, have increased investment in features deemed to deliver the most public goods, such as hedges (Kristensen et al. 2016).

Hedges were removed from intensively farmed arable land to increase cropped area and allow the use of larger machinery. In contrast, more extensive pastoral agriculture led to land abandonment and encroachment of woody species between hedges (Sklenicka et al. 2009). For example, 71% of hedgerows by length were lost between 1959 and 2005 when the remnants of the medieval pluzina landscape in the Plzen region of the Czech Republic were developed (Sklenicka et al. 2009). However, as hedge length decreased, average hedge diameter nearly doubled from 7 to 13 m. Intensification thus increased the disparity between form and function of unmanaged hedges in intensive areas of arable and pastoral agriculture, compared to less productive areas. In Northern Ireland, the heterogeneity of species-rich hedges and small fields in County Fermanagh contrasts with the homogeneity of small hedges around large pastoral fields in County Down. Removal of older administrative boundary hedges exacerbates this effect (Hegarty & Cooper 1994). In contrast, in-farm hedges in France are more often removed than boundary hedges (Blanco et al. 2019).

Bocage is the idealized, hedge-dominated landscape with large hedges and small fields predominating in parts of France, England, Ireland, the Czech Republic, and the Netherlands. Bocage has high conservation interest and thus has been the focus of much research. The flora comprising the bottom of British hedges has historical, management, and ecological disparities from that in woodland, which is more variable (French & Cummins 2001). Despite disparity in ground-plant communities, hedge bottoms should be considered to be a part of the vertical hedge component. Hawthorn, *Crataegus* spp., and blackthorn, *Prunus spinosa*, dominate two-thirds of British hedges, but these common hedge types are the least rich and diverse in herbaceous plants. Early research, however, identified seven hedge types based on management that show an increase in bird species richness from remnant to overgrown with outgrowths (Pollard et al. 1974). Green lanes consisting of two parallel hedges with a central track further enhance heterogeneity. While the outer parts of such hedges do not differ in species composition and richness, the inner hedges of green lanes support more plant and animal species than matched single hedges (Walker et al. 2006).

Hedges are also known as living fences in Central America, where their principal role is stock control. Stone hedges are composed of stone, earth, and plant litter. These can be regarded as hedges as they contain elevated vegetation, and their primary functions overlap with more conventional hedges. The term hedge is also used in tropical systems, where their primary function is prevention of soil erosion and loss of nutrients. In arid areas, hedges run along contours (Adhikary et al. 2017) with interior strips where crops can be grown (intercropping). Parallel lines of vegetation involving alternative planting of grasses and browsed species also constitute a form of intercropping. In Australia (Queensland), river tamarind trees, *Leucaena*, tall long-lived legumes, provide browse for cattle in addition to enhanced gains in soil organic carbon (SOC) and total nitrogen (Radrizzani et al. 2011).

Hedgerow loss also occurred in agricultural systems at lower latitudes but may be offset by new hedges reflecting changes in ownership related to inheritance. In pastoral land of western Niger, 18% of hedge length was lost between 1992 and 2016, but this was offset by new hedges added due to splitting of crop fields by inheritance such that the annual rate of change in hedgerow length was 4% (Hiernaux et al. 2019). While new hedges may contribute immediately to the amount of woody material in a landscape, new hedges are not ecologically equivalent to old hedges, especially where hedge species change. As Canadian hedgerows declined, field sizes doubled, and hedgerow plant communities were degraded due to increased use of agrochemicals. Hedge loss, thus, is not restricted to Europe and does not occur in isolation.

Although similar patterns are observed worldwide, there is considerable global variation in hedge structure and composition due to differences in climate, topography, and agriculture. Primary production and slope gradient play significant roles in determining the presence of hedges and their configuration and density (**Figure 1**). Planted hedges are more important in Europe than

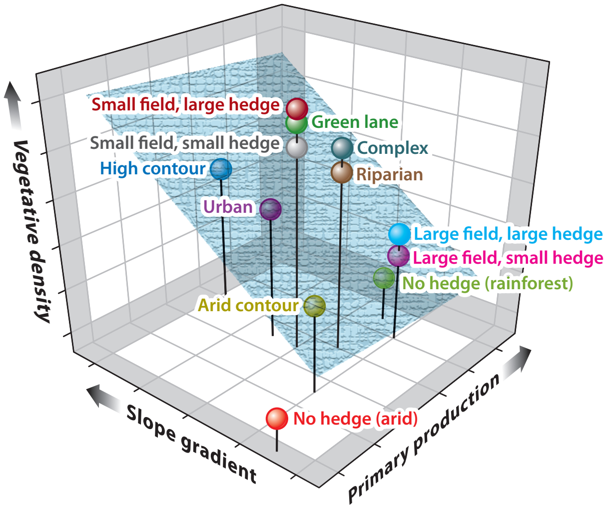

Figure 1

Conceptualized representation of global variation in hedge types (*labeled points*) along hypothetical axes of primary production, slope gradient, and vegetative density. Gray shading indicates environmental extremes unsuitable for supporting hedges, e.g., arid regions with low productivity (*red point*). Note that some regions suitable for supporting hedges may not do so for practicable reasons, e.g., rainforest (*light green point*). The fitted regression plane (*blue texture*) illustrates the relationships between vegetative density, primary production, and slope gradient.

in North America, where the scale of agriculture is larger and wilderness areas continue to exist (Marshall 2005). Thus, hedgerows may be more likely to be long established in Europe than in the United States (Wilkerson 2014). Even at the greatest agricultural production levels, however, lost hedgerows may determine field size and thus continue to affect production (Van Apeldoorn et al. 2013).

ECOSYSTEM SERVICE PROVISION

ESs are the components of the natural world on which we depend and can be divided into provisioning, regulating, cultural, and supporting services (Millenn. Ecosyst. Assess. 2005) (**Figure 2**). There are global differences in the main ESs provided by hedges: Antidrought, antiflood, and antipredator functions characterize tropical hedges, while temperate hedges provide biosecurity, crop protection, pollination, and land ownership demarcation. Historical ESs of uncultivated elements in the landscape (Marshall 2002) may also differ greatly in their current functions, e.g., food and fuel provisioning are largely ESs of the past in developed economies (Barr & Petit 2001). Similarly, structure, composition, and management reflect current hedge functions and local conditions, although past functions may also still be evident. The ratio of hedge area or length to crop area varies enormously depending on topography and risk from too much or too little water. The extent to which hedge composition and ESs are linked is affected by the proportion of seminatural vegetation across agricultural landscapes. Regulating services are positively associated with seminatural vegetation, while provisioning services are more context dependent (Garcia-Feced et al. 2015). Some hedgerow species have multiple uses; for example, vetiver grass, *Vetiveria nemoralis*,

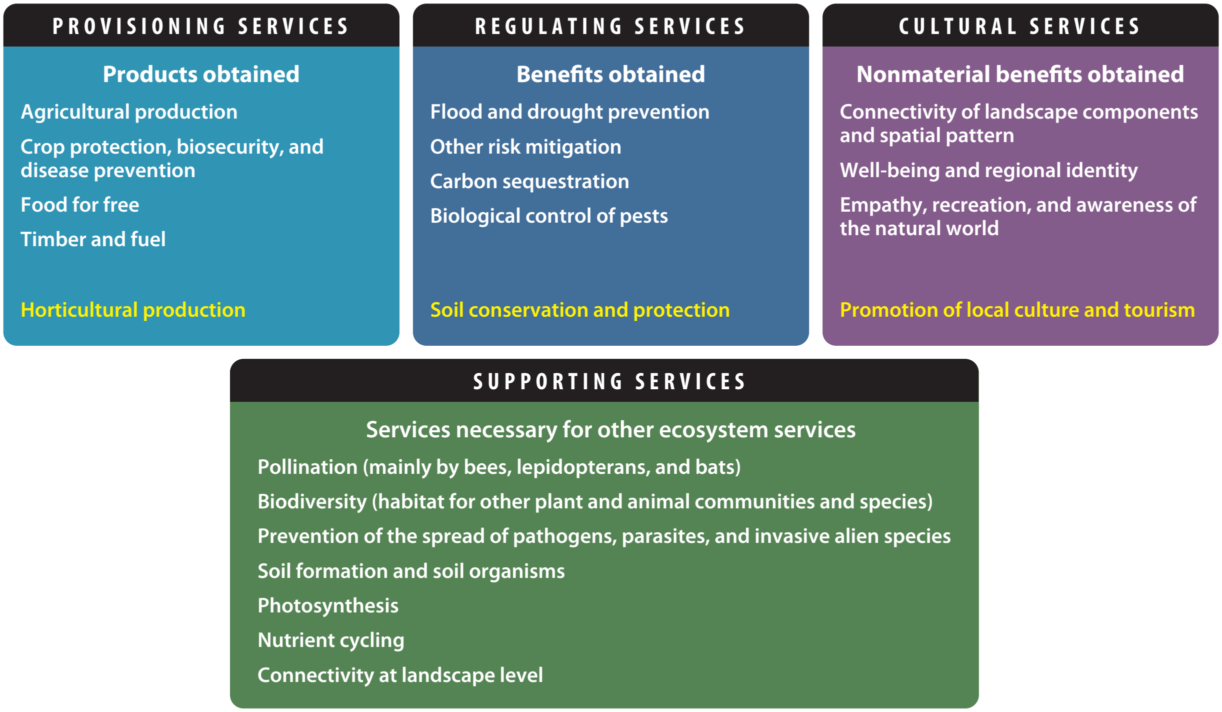

Figure 2

Major ecosystem services delivered by hedgerows, categorized as provisioning, regulating, cultural, and supporting services. The lower group (*yellow text*) in each of the top categories is of particular relevance under conditions of extreme high or low temperature and precipitation, such as are likely to occur with global climate change (Millenn. Ecosyst. Assess. 2005, Dover 2019).

is used as fodder for livestock but also has culinary and cosmetic uses and is a source of pharmaceutical products and building materials. Vetiver is particularly valued for soil conservation as it extracts all but the finest soil particles from water and reduces runoff by up to 88% (Donjadee & Tingsanchali 2013). Soil loss increases rainfall runoff volume, slope, and vertical hedge interval and is predictable with a high degree of accuracy. Field margins, roadside verges, and hedges are interdependent not only with respect to the ESs they provide but also in how they are managed (Marshall 2005) and should be included in an overall evaluation of hedge ESs.

PROVISIONING

Crop Production and Protection

The primary role of hedges around fields is to provide stock or crop protection leading to improved production. This may be a net effect with potential losses in production close to hedges due to competition for water, nutrients, and light and a more expansive increase further from the hedge (Govindarajan et al. 1996). Where water is limiting, e.g., between contour hedges, there can be competition between hedge and crop plants. Shading effects are more important at higher latitudes and in winter. Shade reduces air and soil temperatures and thus may affect growth close to hedges, depending on their orientation, up to a distance of twice the hedge height. Hedges are semi-impermeable to wind, affording shelter to crops growing up to 12 times the hedge height away and reducing wind speed by up to 40%, impacting soil moisture, air temperature, soil temperature, relative humidity, and evaporation (Pollard et al. 1974). Thus, crop production is positively affected by the presence of hedges due to reduced transpiration; this effect will extend further into a field if hedges are taller. Windbreak functionality may be sufficient to make crops economically viable through enhanced yields. In a semiarid part of Kenya, seasonal winds severely erode soil and remove mulch. A live fence of Indian coleus, *Coleus barbatus* (Lamiaceae), in combination with southern silk oak, *Grevillea robusta* (Proteaceae), was used to protect maize intercropped with beans, but variability in wind speed and direction and poor location of gaps in hedges may reduce biomass of hedge trees and crops below their potential (Oteng'i et al. 2000). Windbreak hedges also reduce mechanical damage to crops, enhancing marketability, and reduce erosion of both plants and soil. There are also seldom-recognized benefits in terms of stock welfare that might prolong sustainability on grass as well as reduce time required to reach market weight.

Generally, the net benefits of hedges with regard to yield are difficult to establish (Pollard et al. 1974). A model parameterized by published data suggested that 29% of crop production is lost within a distance of twice the hedge height but production then increases by 6% up to a distance of 20 times the hedge height into the field. Hedgerows intercept the cyclical flow of essential plant nutrients, causing reductions in components including surface nitrogen (69% reduction), subsurface nitrogen (34% reduction), and phosphorus (67% reduction). Nonproduction ESs may compensate for yield loss close to hedges (Raatz et al. 2019). At field level, there is a trade-off between arable crop yield and regulating ESs that depends on field size, hedgerow width, and height (Van Vooren et al. 2017). Intercropping with a legume, such as *Leucaena*, can increase production stability or even lead to yields that exceed those in plots with fertilizer applications (Sileshi et al. 2011).

Timber, Fuel, and Food for Free

Hedges are a source of timber that, owing to shape and growth ring structure, provided frameworks for many medieval buildings and ships. Elm was highly valued with numerous uses including furniture and coffin manufacture (Pollard et al. 1974). After the Second World War, hedges and parks in Great Britain were estimated to contain over 21 million cubic meters of workable hardwood (Pollard et al. 1974). Hedges also provided fuel for local use, but cheap fossil fuels led to a decline in labor-intensive firewood collection. Subsidies for farm woodland and efficient wood burners could make fuel from hedgerows increasingly important for serving farm needs and local community and commercial enterprises. The savings of coppicing hedgerows for wood fuel over 15 years, in comparison to flailing hedges annually, are approximately $160/km/year (Chambers et al. 2019). Remains of plants found in Bronze Age settlements in the French Alps suggest that the gathering of wild, edible seeds and fruit from forest edges and hedges was common. While still a common and widespread source of food in rural areas of developed countries, hedges are possibly used less as sources of food for humans than in the past. However, foraging for hedgerow leaves, fruits, nuts, and fungi is undergoing a revival in response to concerns about agrochemicals and climate change.

REGULATION

Soil Protection

Hedgerow soils provide ESs including storing organic carbon, promoting infiltration and storing runoff, increasing earthworm diversity, and hosting distinctive communities of mycorrhizal fungi and microarthropods (Holden et al. 2019). These effects are more obvious in hedges delimiting arable fields and the contour hedges typical of arid regions and steeper slopes. Shallow trenches along contours with low flanking hedges of *Leucaena* and *Gliricidia* (Fabaceae) in India reduce runoff and soil carbon, nitrogen, phosphorus, and potassium loss in comparison to control crops (Adhikary et al. 2017). *Gliricidia* with grass filter strips reduce runoff and soil loss by a third and produce a fourfold increase per year in SOC and a 49% increase in production of finger millet, *Eleusine corcana* (Lenka et al. 2012).

Even minimal hedges made up of parallel lines of mondo grass, *Ophiopogon japonicas*, can reduce erosion by lowering water runoff and rill formation, preventing or reducing soil nutrient loss and selection for particle size, and stabilizing soil moisture content (Fan et al. 2015). Research on native grass hedges in northern China also suggests that these are effective in protecting soil by reducing runoff and soil loss and are more cost-effective than cultivation terraces (Xiao et al. 2012). Nutrients, with the exception of potassium, and clay particles accumulate on slopes above hedges and are depleted below hedges. Overall, phosphorus accumulates, while SOC and potassium decline (Lin et al. 2009). Contour hedges have also been used to good effect in the humid uplands of Peru, where hedges of the ice cream bean, *Inga edulis*, a nitrogen fixer, reduced soil loss by 93% and conserved water by 83% in experimental plots (Alegre & Rao 1996). Maintaining a protective green crop and hedgerows and not tilling collectively reduce soil loss by 92%, with hedgerows contributing a 33% savings (Frank et al. 2014).

Hydrology and Flood Prevention

Transfer of soil water by hedges depends on dryness, season, and year, with consequent variation in rates of recovery of soil moisture levels. Hedges transfer water laterally, depending on immediate soil water potential gradients, increasing capillary rise and decreasing ground water recharge. This results in greater variability in soil moisture close to hedges compared to further away. Soil water balance on a hill traversed by a hedge in Brittany, northern France, was heavily affected by transpiration in woody plants, with 40% of water output attributable to this source. Increased soil capillary action and decreased soil drainage were also observed when trees were included in model simulations (Thomas et al. 2012).

Carbon Sequestration

Hedge SOC components are more like forest soils than agricultural soils but vary with hedge vegetation characteristics. Overall biomass carbon and CO_2 emissions do not differ between planted and remnant hedges in the Fraser Valley, Canada, although richness and diversity of woody vegetation are greater in the former (Thiel et al. 2015). SOC in planted hedges is 40% greater than in adjacent fields in production. In *Leucaena* and grass pastures in Australia, the amount of carbon accumulated as SOC is sufficient to offset CO_2, CH_4, and N_2O emissions from cattle over 20 years (Radrizzani et al. 2011). Hedges in an upland agricultural area of Kenya constitute the second largest aboveground carbon pool (Henry et al. 2009). Farmers participating in AESs may be highly motivated to improve the appearance and amenity value of their immediate surroundings, but linking incentives for carbon sequestration to the promotion of biodiversity could both benefit ESs and widen AES participation (Henry et al. 2009). Recovery of SOC and other soil characteristics during rehabilitation of degraded lands with hedgerows comprising *Indigofera teysmannii*, Fabaceae, may be affected by slope, aspect, and aggregate size such that reducing runoff by planting hedges is particularly valuable in protecting the SOC and the soil as a carbon sink (Lenka et al. 2012).

Biological Pest Control

Abundance and species richness of pest predators in fields with and without hedgerows are subject to subtle effects. In bocage in Brittany, France, an increase in maize cultivation to support milk production creates a more open landscape than increased cereal cultivation allied with pork and poultry enterprises, creating a dichotomy in beetle communities with forest species predominating where hedges are adjacent to pastoral land and larger species decreasing in numbers in favor of smaller, more mobile, ubiquitous species in open landscapes (De la Peña et al. 2003). In mature bocage, the abundance of carabid species is related to the presence of double hedgerows and trees and herbaceous layer density, while on a landscape level, distance to large areas of woodland is critical (Burel 1989).

Carabids are polyphagous predators associated with new hedges and adjacent intensive fields, but the number of carabid species declines with distance into the field from the hedge center. Beetle abundance declines with agricultural intensification, but abundance of carabids remains relatively stable in hedges, underpinning their vital role in maintaining hedgerow ESs (Brooks et al. 2012). Old hedgerows in Germany contain forest and grassland beetle guilds, but in small and young hedges, this habitat effect is absent. Old hedges provide more niches and have greater functional diversity and more specialized carabid species (Theves & Zebitz 2012). In comparison to nonhedge field boundaries, hedges contain taller, more species-rich vegetation, with more bare earth and higher SOC. These conditions benefit beetles, particularly rove beetles (Staphylinidae), and spiders, which are more numerous in hedgerows, regardless of age (Pywell et al. 2005).

Abundance of herbivores and predators is related positively to foliage density, while detritivore abundance is correlated with hedge gap size (Amy et al. 2015). Hedgerows, particularly continuous hedges with standard trees and diverse flowering plants, support predators that also encroach into cultivated areas. Natural enemies of plant pests such as aphids in cereal fields reach higher diversity in organic than conventional fields but are much influenced by immediate factors such as hedge length and configuration (Puech et al. 2015). Hedges around tomato fields contain more parasitoids and fewer aphids than cropped areas, and this effect extends 100 m into the fields, 200 m where there are multiple hedges (Morandin et al. 2014). Aphidophagous hoverflies encroach into oilseed rape and wheat fields from hedges, particularly where these are connected to forest (Haenke et al. 2014).

Spiders are important predators of pest insects in fields. Spider communities within hedges reflect woodland rather than grassland habitats such that land use within fields influences the dispersal of spiders into the fields and, thus, the ESs they provide (Nardi et al. 2019). Therefore, some species increase in abundance toward hedges and others either do not or differentiate between hedgerow types such as riparian and nonriparian. Spider diversity is greater in wide riparian strips (>50 m), but hedges close to soybean and cornfields (within 15 m), for example, contain spider species that are also found at high densities in agricultural plots and shelterbelts of native plant species (Fukuda et al. 2011).

Hedgerow vertebrates may have considerable benefits with regard to pest mollusks, arthropods, and vertebrates. Bats are major predators of night-flying insects; they follow hedges while commuting to foraging sites and may exploit prey such as moths that also move along hedges (Coulthard et al. 2016). Bats may favor hedgerows with standard trees. While some bat species favor agricultural landscapes with wooded hedgerows, on a local scale others favor poorly stratified hedges with trees (Lacoeuilhe et al. 2018). Bat species inhabiting farmland generally have an affinity with hedges, but a bias against hedges occurs where these are much reduced due to annual cutting (Russ & Montgomery 2002). Different bat species benefit from different management prescriptions for field boundaries; for example, common pipistrelles prefer sites rich in dicots along taller hedges that shelter their prey (McHugh et al. 2019). Hedges also interact with other landscape features; for example, ponds benefit bats, birds, and amphibians.

CULTURE

Hedges as Landscape Components

Species richness of generalist and specialist taxa is related positively to landscape habitat heterogeneity. Combined use of hedges and botanically diverse field margin strips promotes diversity, but some landscape components are more critical than others in supporting biodiversity. In one study, hedgerows and waste ground comprising <5% of land area maintained 11 animal taxa across 12 habitats (Evans et al. 2013). Hedges are widely valued for their role in connecting landscape components such as woods, suburban gardens, and meadows. The environmental conditions and, hence, plant species associated with hedges are akin to woodland edges in lacking plant species that prefer woodland interiors (McCollin et al. 2000). Wider hedges (>12 m) in northern Italy share more forest plant species with adjacent woodlands (Sitzia 2007). The beetle *Abax parallelepipedus* uses hedges to disperse, but distance traveled is longer in hedges with less cover (Charrier et al. 1997). Hedge management, therefore, is important in ensuring connectivity between wooded areas.

The role of hedges in the wider landscape and the need to retain ancient hedges and plant new ones are also recognized where farms and field size are increasing. Local initiatives to increase the efficacy of hedges in providing ESs are less effective than increased hedgerow planting and management on a landscape scale. Enhanced parasitism in aphids (12–18% increase in prevalence) and increased pollinator visitation and seed set (70% increase) are attributable to an enhanced network for the dispersal of beneficial insects (Dainese et al. 2017). Landscape initiatives that promote hedges take little land out of production and thus are regarded as low cost and high benefit.

Networks of hedges at the landscape level may either enhance or reduce dispersal of chemicals, propagules, plants, and animals. Landscapes comprising a mosaic of different habitats potentially aid dispersal of pest and beneficial species, but the effects are hard to predict. The montane vole, *Microtus montanus*, is a pest of apple orchards in British Columbia and Washington State, while the deer mouse, *Peromyscus maniculatus*, is regarded as beneficial, but only the latter benefits from dispersal along linear habitats (Sullivan & Sullivan 2009). Dispersal of animals and plants along hedges connecting woods is two-way, such that plant communities in the latter reflect hedgerow species richness, age, and width (Roy & de Blois 2008). Colonization of hedges by woodland plants is related to the source populations, i.e., areas of woodland, but there is no correlation between plants in hedges, which are generally species rich, and those in fields, which are generally species poor. Recent hedges contain fewer forest plant species than ancient hedges, but most environmental parameters do not differ, suggesting that traditional management of recent hedges will transform these into habitats similar to ancient hedges (Litza & Diekmann 2019).

Health and Well-Being: Aesthetic Value and Empathy with Local Character

Governments and nongovernmental organizations value hedges sufficiently to monitor their status and subsidize their management based on some knowledge of the complicated interactions among the ecological, physical, social, and agronomic factors influencing hedgerow composition and structure (Barr & Petit 2001). How elements of the landscape are valued aesthetically varies between places. Visitors to farmland in Holland and Germany placed a higher value on hedgerows and lines of trees than on tree clumps and crop diversity and vice versa, respectively (Van Zanten et al. 2016). Hedgerow length has a positive effect on spatial network cohesion but may incur costs and might involve replacing mature hedges, thus undermining the cultural heritage of the site. The cost of planting and managing new hedgerows suggests it might be preferable to improve existing hedges using traditional management techniques (Barr & Petit 2001). Cultural values relating to hedges, however, are not immutable; for example, the use of traditional pollard trees in hedges has been abandoned in favor of shaping the trees (Lotfi et al. 2010).

Rural hedgerows constitute a major seminatural habitat with a wide range of taxa and ecological processes reminiscent of woodland and grassland ecotones. Properly managed hedgerows provide an experience of the natural world for residents and visitors. Landscapes that present well-managed hedges attract tourists, e.g., during spring blossom season, harvest, and the breeding season of hedgerow birds, creating an accessible, affordable experience for people more used to urban settings. There is inadequate information on the attitude of visitors and residents to landscapes where hedges are an important component. People in a protected landscape of southwestern Germany have an appreciation of nature and biodiversity associated with features such as hedges, but these views are affected by socioeconomic effects like age and residency. Similarly, social pressure based on attitudes of neighbors affects farmer attitudes to prescriptions under AESs, including the maintenance of hedgerows (Gatto et al. 2019). Awareness and promotion of traditional, local hedge-management practices are important in sustaining biodiversity and empathy with local landscapes (Fukamachi et al. 2011). Outreach and technical support are also critical in promoting hedge restoration and farm sustainability, which in turn provide benefits to farmers. For instance, uptake of hedge restoration led to better pest control and crop pollination with a return on investment within 7–16 years (Long et al. 2017).

SUPPORT

Biodiversity

Conservation evaluation of hedges is often based on plant species richness or diversity (French & Cummins 2001). Age is an important factor with regard to biodiversity and species composition. In southern Britain, the number of plant species in 30 m of hedge is approximately one per 100 years of age (Pollard et al. 1974), but plant species richness may also be high in recently planted hedges. These tend to be dominated by grasses and ruderal species, whereas both seed banks and vegetation of ancient hedges are dominated by stress-tolerant woodland species (Hegarty & Cooper 1994). Over 330 animal species were found to depend on seed as a food source on an organic farm, but seed samples from uncultivated areas are more species rich and have greater biomass and energy content than cropped areas (Evans et al. 2011). This rich source of seed declined with simulated increased agriculture intensification, which in turn impacted parasitoid abundance.

Butterflies associated with hedgerows are mostly common species, but species richness may be high, with 39 hedgerow species, including 64% of recorded British species (Dover & Sparks 2000). Hedges generally contain only woodland plant species with wider tolerances, lacking more specialized woodland species as woodland conditions are not replicated in hedges (Barr & Petit 2001). The ground level of hedges in pastoral farmland may have more species than hedges in arable land, which are cultivated and sprayed with herbicide. Pastoral hedges, however, may be less species rich due to phosphate enrichment, overgrazing, trampling, and browsing (Wright 2016).

Generalist mammals exploit hedgerow systems more than specialist woodland species and can maintain populations in isolated hedges (Schlinkert et al. 2016). Wide, continuous hedges composed of native species maximize connectivity for arboreal and fossorial mammals (Dondina et al. 2016). In Brittany, the diversity of small mammals is least and the abundance greatest in hedges in intensified agricultural land, but species preferences confounded the overall effect; for example, pygmy shrew, *Sorex minutus*, preferred less intensive agriculture, while bank vole, *Myodes glareolus*, preferred more intensification (Michel et al. 2006). Frugivorous mammals and birds disperse seeds from fresh fruit along linear features suitable for shrub establishment, potentially aiding the dispersal of invasive plant species (Suárez-Esteban et al. 2013).

The importance of hedgerows to farmland birds is well established. In the Central Valley of California, there are two to three times the number of bird species and three to six times the number of birds in hedgerows, tree lines, and riparian woodland than along field margins (Heath et al. 2017). Some five million pairs of birds breed in hedgerows in the United Kingdom (Newton 2017). Whether management of the composition of land in production or enhanced heterogeneity of the landscape as a whole maximizes bird species richness and abundance is debatable. Steppe and farmland species benefit most from management and land use in south Portugal, while the presence of more natural components of the landscape favored birds of woods and shrub (Santana et al. 2017). Bird communities associated with woodland and isolated hedges and those associated with forest are distinct, suggesting the importance of both at the landscape scale (Batary et al. 2012). Farmland hedges lie along a spectrum from tall and wide with frequent trees to short, narrow, and treeless (Barr & Petit 2001). Thrushes, tits, crows, and finches (22 species) are associated with the former, while just four favor the latter, highlighting minority specialist habitat requirements (Green et al. 1994). Adjacent land use may also be important; most species prefer oilseed rape, and spring-sown wheat is the least preferred crop. Reduced pesticide use in fields, presumably leading to better feeding opportunities, is associated with lower incidence of greenfinch, robin, and song thrush in adjacent hedgerows (Green et al. 1994). In grassland-dominated sites, hedges and other woody vegetation remain vital to grassland specialists. Removal of hedgerows and scrub, prevalence of permanent grassland with livestock, and under-field drainage systems, for example, reduce nesting and foraging opportunities and contributed to the decline of the song thrush, *Turdus philomelos* (Peach et al. 2004).

Net benefits of ESs due to birds are difficult to assess. Birds eat farmed Californian strawberries but also reduce numbers of insect pests. However, both the quantity and quality of strawberries are improved adjacent to interconnected hedgerows compared to isolated hedges and grassy banks (Castle et al. 2019).

Pollination

Hedges are essential in providing food for the increasing human population (Nicholls & Altieri 2013). Pollinators are responsible for 35% of global crop production of >800 plant species. Many pollinator species use hedges and grassy verges (Phillips et al. 2019). Floral diversification in hedgerows increases the efficacy of pollination. Hedgerows surrounding organic cider apple orchards in northern Spain contained 63 species visited frequently by pollinators (38% of all insects) (Minarro & Prida 2013). Intensive agriculture has a strong negative effect on pollinators (Happe et al. 2018), and noncrop areas free of fertilizer and pesticides support more pollinators, depending on taxon. In Germany, solitary bees benefit from organic agriculture, while bumblebees benefit from small-scale, conventional agriculture (Happe et al. 2018). Hedge age promotes the diversity and abundance of pollinators, particularly rare, specialist species, which are associated with increasing floral diversity, although this effect levels off with hedge maturity (Kremen & M'Gonigle 2015, Kremen et al. 2018). Flowers in the lower part of hedges are a food resource for pollinators and, critically, aid dispersal in intensive farm landscapes. Hedgerow flowers disproportionately provide nectar for wild bees and are an important component of nectar phenology (Timberlake et al. 2019). Bees, however, require access to a range of nutritional elements for larval development and reproduction, suggesting that a rich hedgerow flora is beneficial (Filipiak 2019).

It is not always clear whether the presence of hedges has a positive effect on crop yield. An experimental investigation of seed set in sunflowers, *Helianthus annuus*, showed an interaction between wild and managed bees but no role per se for hedges (Sardinas et al. 2016), leading to the conclusion that the benefits of hedges may be subject to crop and regional effects. Roadside verges are havens for grassland insects, especially where they are shielded from chemicals by hedges. The number of bee species is related to the number of native plants, mainly because verges are unplowed and hence are suitable as breeding habitat for ground-nesting bees (Hopwood 2008). Most research on the role of hedgerows in crop pollination is conducted in intensive, temperate systems, but there is evidence that beneficial effects also occur in warmer settings; for example, hedgerow bee species in Arizona are more similar to those in woodland than in fields (Hannon & Sisk 2009), and 82 bee species inhabit hedges in Kenya (Mwangi et al. 2012).

Soil Biota of Hedges

Five times the number of earthworm casts were found in shaded areas under *Leucaena* hedges in intercropping systems compared to the exposed crop area (Hauser 1993). Casts contained three times more essential plant nutrients, nitrogen, potassium, calcium, and magnesium, suggesting worm casts play a key role in nutrient cycling in the cropped area. Soil chemistry, reflected by microbial biomass, carbon and nitrogen content, enzyme activity, and phosphate content, differs markedly between arable fields and surrounding hedges and between hedges on organic and conventional farms (Monokrousos et al. 2006). Bacteria, fungi, and microarthropods also differ within soils beneath hedgerows in comparison to open fields, suggesting that hedgerows provide a reservoir of soil biodiversity (Spaans et al. 2019).

Disease and Invasive Alien Species

Rodents and lagomorphs, which are known to carry pathogens including *Salmonella*, *Giardia*, and *Cryptosporidium*, increase in hedgerows around walnut orchards in California, but there is no indication of any effect on crop yield or contamination by food-borne pathogens (Sellers et al. 2018). Numbers of small rodents are often higher along hedges than in other habitats. The association of small rodents with hedges may facilitate the spread of tick-borne diseases where landscapes are characterized by high connectivity (Perez et al. 2016). Hedges may also attract disease vectors in certain parts of their range. European badgers, *Meles meles*, which carry bovine tuberculosis, a major economic threat to farming, use hedgerows and forage more on field boundaries in some parts of Europe compared to Britain (O'Brien et al. 2016, Pita et al. 2020).

Hedgerows may support invasive plant and animal species. Planting hedges with trees may control the rate of spread of the common reed, *Phragmites australis*, an invasive species found along roads in Quebec, Canada (Jodoin et al. 2008). Invasive species may be few compared to native species in hedges, but their potential impact is great, even in areas of extensive agriculture. Appropriate management can potentially curb their spread, depending on community pattern as well as species traits (Wilkerson 2014). However, the distribution of the black cherry, *Prunus serotina*, a native of North America, is related to the high level of connectedness in the bocage in Flanders, Belgium, owing to avian seed dispersal (Deckers et al. 2005). In Ireland, hedges facilitate invasive mammals. The European hare, *Lepus europaeus*, makes more use of hedges to shelter than does the native Irish hare, *Lepus timidus hibernicus* (Caravaggi et al. 2015), and nonnative bank voles and the greater white-toothed shrew, *Crocidura russula*, are associated with reduced numbers of wood mice, *Apodemus sylvaticus*, and the disappearance of the pygmy shrew, *Sorex minutus* (Montgomery et al. 2015).

MANAGEMENT AND RESTORATION

Despite the fact that hedgerows often are the only common, seminatural habitat in a given area, they may fail to deliver ESs. Deterioration in hedge quality and floral diversity was driven by management rather than linked directly to a 60% increase over 70 years in intensively farmed land in southern England (Staley et al. 2013). Conventional management involves a transition from coppicing and laying, a process involving partially cutting through, bending, and fixing growing stems that dates back to the Romans, to no management or frequent, mechanized cutting. Coppicing is used less frequently, and the effects of different methods of laying hedges have converged over time such that cheaper, mechanized methods are considered as effective and more economically viable than traditional laying. These reduced costs mean that the length of hedges rejuvenated under AES could double (Staley et al. 2015). Neglected hedges develop gaps that significantly affect plant and animal diversity (MacDonald & Johnson 1995).

Structurally, hedges vary from being large in volume and ecologically diverse to small in volume and lacking in diversity at all levels. Enhanced botanical diversity, rotational cutting regimes, and integrated management of field edges and hedges offer considerable conservation benefits even in the absence of definitive research. AES options often include less frequent cutting of hedges, with closed seasons for cutting to facilitate hedge-nesting birds; however, these closed seasons may not be sufficiently specific or enforced to be effective (Porter 2017). Structurally complex hedges that are infrequently cut produce more berries in winter, sustaining overwintering birds (Chamberlain et al. 2001). Cutting every third year in winter enhances hawthorn and blackberry production (Dover 2019). Invertebrates respond to botanical composition, structural diversity, and shelter. Only concealed moth larvae (mining, tent-forming, and case-bearing larvae) are more abundant, and rates of parasitism are higher, where there is less cutting, with increased moth species richness and diversity in winter-cut hedges (Facey et al. 2014). Four declining moth species in Britain benefit from less severe cutting regimes (Froidevaux et al. 2019). Bats also benefit from longer intervals (3–10 years) between hedge cutting because of increased dipteran prey abundance (Froidevaux et al. 2019).

Reduction in chemical use enhances biodiversity, but only one family of moths in North America is more numerous on organic than conventional farms (Boutin et al. 2011). Chemical pesticides reduce the abundance of target and nontarget species associated with hedges and indirectly affect species numbers and breeding success at higher trophic levels. Hedgerows of organic farms contain more associated plant species than comparable hedges on matched, conventional farms (Aude et al. 2003). This effect is attributed to reduced pesticide drift and greater immigration of species on organic farms. Hedges with 6-m-wide unsprayed conservation headlands have lower pesticide levels than hedges without such strips. Predators penetrate cropped areas more successfully where such strips exist.

In a long-term study of pollinators in the Central Valley of California, restoration of hedges composed of native plants increased diversity by 14% relative to other field margins (Ponisio et al. 2016). Using flowering hedgerows enhances colonization and persistence of bees and hoverflies between seasons compared to unrestored field margins. Tailoring habitat prescriptions for particular insect guilds in small-scale restoration schemes is critical to their success (Kremen & M'Gonigle 2015). Hedgerows provide prominent, denser foraging opportunities for honeybees and present more effective cues for orientation and navigation (Menzel et al. 2019). Hedgerow restoration and appropriate management should increase the abundance of native species, since pollinators generally prefer these over exotic plant species. Reduced costs and improved pollination can make a 300-m hedgerow restoration profitable within 7 years (Morandin et al. 2016).

The efficacy of hedge management may be confounded by other factors. In Germany, hedge height and width had no effect on the richness and abundance of woodland and farmland birds, but mean hedge width was >4.0 m and height >3.5 m (Batary et al. 2012). Studies on more heterogeneous hedges show a direct relationship between hedge size and bird species richness and abundance (MacDonald & Johnson 1995, Hinsley & Bellamy 2000). Further increases in species richness and diversity are associated with management efforts that promote hedge complexity, for example, maintaining low-level cover at the base of hedges by excluding stock and agrochemicals, while enhancing associated features such as ditches and wildflower strips (Hinsley & Bellamy 2000).

Benefits of AESs aimed at nonproductive areas such as hedges may extend to other habitats and the wider landscape. Creating and maintaining a range of seminatural habitats generally increase the abundance of a range of pollinators and predators. At the landscape level, greater cover by hedgerows in intensive farmland in northern Italy is associated with enhanced aphid parasitism (increased by 12–18%) and seed set (increased up to 70%) independent of local field margin conditions (Dainese et al. 2017). Increased nutrient input negatively affects hedge shrub and herbaceous species richness, while grasses and arable weed species increase. Shading in hedges determines the composition of the associated ground flora, and careful management can prevent the encroachment of invasive alien plant species (Wilkerson 2014) or ensure that particular plant species flourish (Minarro & Prida 2013). Cutting to allow light in, sowing seed of perennial species, applying selective herbicides, and excluding fertilizers restore floral diversity at the base of hedges (Maudsley et al. 1998).

Introducing complexity at the base of a hedge has a direct positive effect on biodiversity. Ditches and banks provide shelter for larger predators (e.g., snakes, amphibians). Some arthropods and reptiles colonize new hedges rapidly if provided with banks created from local soil (Lecq et al. 2018). Hedge planting on existing verges increases species richness of plants but not necessarily that of other taxa in areas of intensive agriculture (Le Viol et al. 2008), possibly due to the discrete nature of hedge and grassland communities. There may be increases in taxonomic and functional trait diversity at the landscape level, suggesting that a mosaic of planted hedges and grassland is beneficial, for example, in managing rural road systems.

At least a third of species of conservation interest, including all vertebrates and some critical pollinators, discriminate useful space on a landscape scale, greater than the average farm size, requiring multiple farmers to work together. Hedgerow restoration at this scale results in greater heterogeneity in hedge maturity and associated communities (McKenzie et al. 2013). There is a strong case for efforts to promote hedgerow restoration to be coordinated regionally to protect unique landscapes and habitats, e.g., the North Downs of southeast England, southern Sweden, and the Champsaur in the French Alps (Barr & Petit 2001). The restoration of green lanes has been proposed as part of a European Greenway system (Carlier & Moran 2019), emphasizing the benefits of integrating productive agricultural systems, hedgerows, and other seminatural elements on a much larger scale.

The interactions between ESs and AES prescriptions related to hedgerows in temperate systems suggest that many prescriptions benefit multiple ESs, with most benefitting both crop production and biodiversity, others soil conservation and biological control, with only carbon sequestration subject to singular, independent effects (**Figure 3**). For example, restoration of pollinator habitat benefits a wide range of ESs associated with biodiversity and production (Wratten et al. 2012).

URBAN HEDGES

There are comparatively few studies of urban hedges, and their value is underestimated. Urban hedges are often composed of nonnative species that support different invertebrate communities from rural hedges but are, nevertheless, important for wildlife (Fukamachi et al. 2011, Lecq et al. 2018). Isolated trees in urban hedges can produce allergenic effects by producing disproportionally more pollen (Kasprzyk et al. 2019). Urban hedges reduce dominance of hard surfaces,

a

Metrics	PC1	PC2	PC3
	Axes		
Eigenvalue	5.806	1.674	1.159
% variation	49	21	13
Cumulative % variation	49	74	86

Ecosystem services	PC1	PC2	PC3
	Axes loadings		
Health and well-being	0.958		
Crop production	0.877		
Biosecurity	0.874		
Biodiversity	0.871		
Connectivity	0.865		
Pollination	0.776		
Flood mitigation	0.563		
Soil conservation		0.969	
Biological pest control		0.890	
Carbon sequestration			−0.932

b

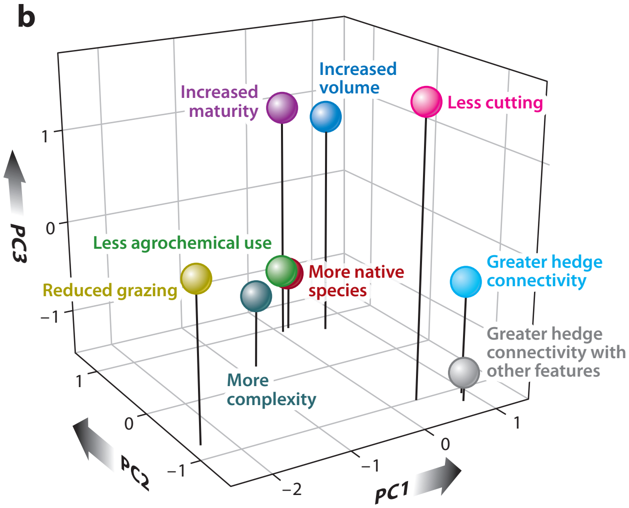

Figure 3

(*a*) Principal component (PC) axes loadings capturing multicollinearity in the ecosystem services delivered by hedges, including crop production, biosecurity, flood mitigation, soil conservation, biological pest control, connectivity, health and well-being, pollination, biodiversity, and carbon sequestration. (*b*) Conceptualized relationship of ecosystem service principal components with hedge management. Each labeled point represents an agri-environmental scheme prescription.

reducing flash flooding, as well as acting as barriers to noise and air pollution (Dover 2019). Privacy and access to contemplative space are additional services of urban hedges. Provisioning ESs are also delivered by hedges in urban environments, e.g., small-scale vegetable, fruit, and honey production. The visual and microclimatic effects of urban hedges affect use of open spaces, reduce maintenance and energy costs by reducing wind chill, and improve health by encouraging walking. Urban landscapes may be planned to maximize ESs, especially well-being, through continuity with other aspects of green infrastructure, including riparian woodland, urban forests and parks, and the transition zone between countryside and city (Pirnat & Hladnik 2019).

HEDGES AND CLIMATE CHANGE

Hedgerows mitigate climate change through carbon sequestration, improved flood control, and moderation of microclimates. Hedge creation connecting isolated stands may facilitate range expansion of species that are increasingly threatened by climate change. Wind damage is an increasing problem for crops. Hedges mitigate the effects of wind and also reduce water requirements of crops (Adeloye & Dau 2019). Windbreak hedges reduce storm damage and improve water use efficiency by slowing wind speed, increasing dew formation, and reducing evapotranspiration. The changing physiological and ecological traits of bird communities suggest that less intensive agriculture and maintenance of seminatural habitats aid generalist and specialist farmland birds affected by rapid climate change (Gauzere et al. 2020).

Hedgerows, intercropping, and parklands collectively cover approximately 1 billion ha (Cardinael et al. 2018). These have significant potential to sequester carbon as biomass and SOC without a loss of food production; conversion of cropland to agroforestry is estimated to benefit SOC by a factor of 1.25 and grassland to agroforestry by a factor of 1.19 (Cardinael et al. 2018). Hedgerow systems protect SOC as climate change progresses but are highly sensitive to intensification (Van Vooren et al. 2017). Remote sensing using lidar can potentially resolve three-dimensional structures, enabling the estimation of aboveground biomass. In Roscommon, Ireland, over half the hedges contained <4 tC/ha, and unmanaged, planted hedges capture 3.3 tC/ha annually (Black et al. 2014). Aboveground biomass varies positively with hedge height and width (Axe et al. 2017): 3.5-m-high hedges contain an average of 42.0 tC/ha, 1.9-m-high hedges contain 32.2 tC/ha, and a 4.2-m-wide hedge contained 9.7 tC/ha more than a 2.6-m-wide hedge. Belowground biomass was estimated as 38.2 tC/ha for 3.5-m-high hedges. SOC, however, varies considerably across all hedgerow landscapes and with depth and age (Radrizzani et al. 2011).

Clearly, hedges contribute significantly to reducing atmospheric carbon, but this is difficult to quantify. Falloon et al. (2004) suggested that hedges in the United Kingdom could sequester up to 2.4% of carbon emissions and 20% of the commitment at that time to emission reduction, with added benefits from conservation headlands and tree lines, and a reduction in N_2O emissions. Agroforestry has the potential to sequester up to 44% of greenhouse gas emissions from agriculture in Europe (Kay et al. 2019). Reducing the frequency of cutting would be a rapid contribution to zero-emission agriculture.

FUTURE RESEARCH

Although there is wide geographical interest in research on hedges, there are biases in subject matter and location. Tropical and subtropical agriculture and horticulture are more concerned with the use of hedges in water and soil management, whereas there is strong interest in biodiversity conservation and ESs in temperate zones. Overall, there is a publication bias toward Europe, especially the United Kingdom, and North America (Haddaway et al. 2018). However, there is insufficient work on the direct and indirect benefits of hedges for agricultural production and quality and stock production and welfare. Integrated management of the provision of a range of ESs requires urgent consideration on a regional scale, given recent increased concern regarding food security, remediation of biodiversity loss, and carbon sequestration. The potential role of hedges in carbon sequestration and flood control should be established quickly, especially under more extreme conditions. Landscape components such as the role of hedgerows in the dynamics of nitrates entering freshwater systems are poorly understood (Thomas et al. 2019). Research is needed to identify the causal processes surrounding adoption of AESs and the key interactions among AES prescriptions and their direct effects on ESs that are likely to lead to increased yields with lower chemical inputs. The impact of hedgerows on the genetic structure of populations, or indeed on the plant species comprising a hedge system, is uncertain. Hedgerow species can exhibit marked genetic variation with low differentiation, suggesting extensive gene flow of both seed and pollen. This is critical due to the emergence of virulent plant pathogens and pests and the fact that many hedgerow trees are in poor health with high mortality levels (Spaans et al. 2018).

Despite long-term interest in the ecology of hedges, there is a lack of appreciation of the wide range of services they provide worldwide and a failure to recognize them as ecosystems in their own right, as well as general management negligence. The interaction of management prescriptions with various ESs is poorly researched, and a more holistic approach is warranted. Interdisciplinary research will undoubtedly reveal how imaginative and sensitive management of hedges and hedgerows at both habitat and landscape scales can help address major environmental problems, restore biodiversity, and mitigate the impacts of climate change.

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