Effects of hedgerows on the preservation of spontaneous biodiversity and the promotion of biotic regulation services in agriculture: towards a more constructive relationships between agriculture and biodiversity

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Abstract

Central to the agroecological transition is biodiversity, which, once restored in agroecosystems, should provide multiple ecosystem services that result from the interactions between different organisms. However, the diversity of expected services raises questions about the capacity of agroecosystems to simultaneously provide many of them as well as the possible existence of synergies and antagonisms. In particular, the relationships between crop-associated biodiversity (i.e., biodiversity in action in crops) and spontaneous biodiversity (i.e., biodiversity not directly related to agriculture) remain unclear. In this article, we analyse the impact of hedgerows on the preservation of spontaneous biodiversity, on the promotion of biotic regulation services such as pollination and pest control in agriculture, and on the interactions between spontaneous and associated biodiversity. Our analysis of the scientific literature shows that hedgerows are unique assets for the preservation of spontaneous biodiversity, while they also provide biotic regulation services to adjacent crops but only under specific conditions, which need to be better understood. We propose a functional conceptual model of the ecological effects of hedgerows on associated biodiversity and we highlight the possible synergistic and antagonistic effects related to hedgerow characteristics and the life-history traits of the organisms under consideration. Our analysis therefore seeks to overcome the cleavage between associated biodiversity and spontaneous biodiversity. This approach is in keeping with a more harmonious relationship between agriculture and biodiversity.

Keywords: hedgerows; spontaneous biodiversity; associated biodiversity; biotic regulation services in agriculture; biodiversity services; agroecosystem functioning

1. Introduction

Biodiversity loss due to ecosystem destruction, natural resource overexploitation, invasive exotic species, climate change, and pollution is a major issue of the 21st century (IPBES 2018). Agriculture, which accounts for 40% of the world's non-frozen land surface, is an important driver of biodiversity loss through deforestation and natural habitat destruction as well as a major source of soil, water, and air pollution (MEA 2005). In particular, intensive agriculture has led to a simplification of farming systems and landscapes, which has largely contributed to the loss of farmland biodiversity (Donald et al. 2001; Green et al. 2005; Butler et al. 2007). A new form of agriculture is thus needed (Mace et al. 2012), based on agricultural practices that promote biodiversity in agricultural landscapes (Norris 2008; Gonthier et al. 2014; Dudley and Alexander 2017). To date, two main contrasting land-use strategies have been proposed (Fisher et al. 2008; Phalan et al. 2011; Folberth et al. 2020): land-sparing (separating biodiversity protection areas from areas of intensive agriculture) and land-sharing (promoting both in the same area through wildlife-friendly agricultural practices). Beyond these strategies, recent studies have highlighted that promoting biodiversity in agricultural landscapes require vast areas of land spared by human activities as well as a favourable agricultural matrix (Kremen 2015; Grass et al. 2020; Torres et al. 2020). This agricultural matrix includes an abundance and diversity of semi-natural habitats in good conservation status (Griffiths et al. 2008; Poux et al. 2010; Duflot et al. 2015; Dainese et al. 2017).

Agriculture in the 21st century is also under pressure to abandon the use of synthetic inputs while providing a number of different ecosystem services: supporting services, regulating services, provisioning services, and cultural services (MEA 2005). From an agroecological perspective, restored biodiversity in agroecosystems is expected to provide many of these services (Tilman 1999; Altieri and Rogé 2010; Wezel et al. 2014). Regulating services correspond to the processes that regulate the environment of the agroecosystem, for example air and water purification, mitigation of floods and drought, crop pollination and the regulation of pest outbreaks and diseases (Mengist et al. 2020). Regulating ecosystem services depend on the ecological functions performed by a functional diversity of beneficial organisms such as pollinators or natural enemies. The need to protect biodiversity in agricultural landscapes is therefore twofold: ensuring the provision of ecosystem services and protecting biodiversity *per se*. Although the relationship between biodiversity and ecosystem services is complex and needs to be studied further (Mace et al. 2012), agroecosystem diversification is usually regarded as a means to harness biodiversity to maximise ecosystem services in agroecosystems. Many studies focus on the impact of crop and landscape diversification as well as agroecological infrastructures on biotic regulation services (Benton et al. 2003; Rusch et al. 2010; Fahrig et al. 2011; Vasseur et al. 2013; Holland et al. 2017; Rega et al. 2018; Sirami et al. 2019; Raderschall et al. 2021). Diversification practices may involve the crops themselves, their spatial and temporal organisation from the field to the landscape scale, and the whole range of organisms purposefully introduced into the agroecosystem by farmers. These organisms are referred to as "planned biodiversity" (Perfecto and Vandermeer 2008; Brustel et al. 2018). For example, cultivar mixtures of cereals can reduce fungal disease epidemics compared to equivalent monocultures (Mundt 2002; Vidal et al. 2020), or diverse soil microbial communities can impede the survival of soil pathogens, forming pest-suppressive soils (Weller et al. 2002; Schlatter et al. 2017). Diversification may also concern the communities living in the agroecosystem that either originate from the agroecosystem itself or emigrate from nearby natural or semi-natural habitats. These organisms, which interact with crops, are referred to as "associated biodiversity" (Perfecto and Vandermeer 2008; Brustel et al. 2018). For example, field margins can favour the presence of pollinators in crops (Garibaldi et al. 2014) or the presence of natural enemies of crop pests (Albrecht et al. 2020). Field margins can be managed to benefit key species for agricultural crops (Smith et al. 2008).

Diversification is therefore slowly becoming a new paradigm of 21st-century agriculture, with the aim to both protect spontaneous biodiversity and foster regulation services rendered by associated biodiversity. Yet until now, biotic regulation services and the protection of spontaneous biodiversity ("biodiversity services") have been studied separately in agricultural contexts, sometimes even opposing scientific communities as to the respective importance of one or the other. Going beyond this dichotomy is crucial to develop a systemic and multi-functional vision of agroecosystems.

Semi-natural habitats are important levers to promote both associated and spontaneous biodiversity in agricultural landscapes. For example, flower strips or grass field margins are well known for providing several regulation services (Díaz et al. 2006), including pollination and bioregulation of crop pests by natural enemies (Holland et al. 2016; Holland et al. 2017; Rega et al. 2018; Martin et al. 2019) as well as spontaneous biodiversity (Duelli and Obrist 2003; Harlio et al. 2019). The establishment of semi-natural habitats has already been widely recommended as part of many agri-environmental schemes in Europe (Kleijn et al. 2006; Batáry et al. 2010; Whittingham 2011; Arponen et al. 2013; Scheper et al. 2013; Berg et al. 2019; Rotchés-Ribalta et al. 2021). However, despite their potential positive effect on biodiversity and regulation services, vast surfaces of semi-natural habitats come at a cost of cultivated surfaces as part of an agriculture-biodiversity trade-off (Kremen 2015; Macchi et al. 2020).

In this regard, hedgerows are particularly interesting amongst semi-natural habitats. Hedgerows are perennial structures requiring little management (Staley et al. 2012), that are found in many agricultural environments across the world (Burel 1996; Baudry et al. 2000; Dover 2019), often occupying the narrow strips between fields that are sometimes difficult to cultivate. In industrial countries, most hedgerows have been destroyed in the past 70 years, as a consequence of the simplification of agricultural landscapes that came with the Green Revolution. In France, since 1950, 70% of hedgerows have disappeared from the bocage (Baudry and Jouin 2003). This amounts to the destruction of 750,000 km of hedgerows under the combined effect of agricultural reparcelling and land-use changes. Although some regions have retained high densities of hedgerows corresponding to earlier levels (between 125 and 200 metres per hectare in the north-west), on four-fifths of the national territory, the density of hedgerows is now less than 75 m/ha, and even less than 20 m/ha on a quarter of the country (IFN 2007). But hedgerows are nowadays receiving renewed interest. They have been the subject of numerous studies, particularly recently in the context of the agroecological transition regarding the provision of regulation services (Holland et al. 2016; Albrecht et al. 2020) or biodiversity protection (Dover 2019).

In this paper, we review the scientific literature with the aim to analyse the relationships between hedgerows, the preservation of spontaneous biodiversity, and the provision of biotic regulation services. We focus on two biotic regulation services, namely pollination along with pest and weed regulation in an agricultural context. Other regulation services provided by hedgerows, such as the reduction of soil erosion (Wu et al. 2010; Fan et al. 2015) or the control of residues of plant protection products will not be addressed here (van de Zande et al. 2004; Lemieux and Vézina 2011) We seek to gain some understanding of the multiple ecological effects of hedgerows on biocontrol and pollination in agricultural landscapes and identify possible antagonisms and synergisms between spontaneous and associated biodiversity in hedgerows, adjacent or more distant fields in the landscape. We review the scientific literature on the ecology of hedgerows to understand what makes them unique among semi-natural habitats in their ability to protect and foster spontaneous biodiversity. We also analyse the literature on the regulation services provided by the hedgerows in agriculture. We eventually focus on the relations between hedgerows, spontaneous and associated biodiversity, and the possible synergies or antagonisms between biotic regulation and biodiversity. We propose a functional conceptual framework of the ecological effects of hedgerows associated with biotic regulation and biodiversity services.

2. An ecological description of hedgerows as ecotones.

In this paper, we follow the definition of hedgerows given by Dover (2019): a hedgerow is a linear stripe of vegetation, including woody elements like trees and shrubs, and herbaceous margins. This section aims at characterizing hedgerow habitats from an ecological point of view.

2.1 The structural heterogeneity of hedgerow vegetation provides a diversity of microhabitats

Hedgerows come under a great variety of forms. Trees may be more or less abundant in hedgerows or may even be absent, but shrubs and herbaceous margins are always present. Good-quality hedgerows include all three vegetation layers. The herbaceous margins are known as fringes, saums, or hems, the shrub layer as thickets, and the tree layer, including some shrubs, as the mantle or coat (Figure 1).

To emphasise the botanical diversity of hedgerows, it should be noted that although they are considered full-fledged habitats in natural habitat classifications (McCollin et al. 2000) (French and Cummins 2001), hedgerows do not correspond to any phytosociological syntaxon. Indeed, the diversity of vegetation types within a hedgerow is such that the hem, thicket, and mantle can each be linked to a different phytosociological syntaxon but not the hedgerow as a whole. Thus, a hedgerow on calcareous soil in the Paris basin can bring together species belonging to syntaxa as varied as *Geranion sanguinei* Tüxen in Müller 1962 or *Trifolion medii* Müller 1962 (hem), *Berberidion vulgaris* Br.-Bl. 1950 (thicket), and *Quercion pubescentis - sessiliflorae* Br.-Bl. 1932 (mantle) (Bournérias et al. 2001; De Foucault and Royer 2015). A hedgerow in a good state of conservation is botanically diverse and is characterised by the structural complexity of the vegetation. This small-scale structural heterogeneity of the vegetation will provide massive diversity in microhabitats for other organisms such as arthropods. The presence of specific structures such as embankments, ditches, or ponds within hedgerows also increases microhabitat diversity and therefore biodiversity (Lawton et al. 2010; Lecq et al. 2018).

2.2 Hedgerows alter local microclimate

Hedgerows profoundly modify the microclimate in their vicinity. Their effect depends on parameters such as the orientation of the hedgerow, the direction of prevailing winds, and the height and width of the hedgerow (related to the presence and abundance of trees). The sunny and upwind sides of the hedgerow will experience greater heat input, higher air and soil temperatures during the day, dryer air, and increased temperature contrast. By contrast, the shady and leeward sides of the hedgerow will experience greater soil moisture and relative air humidity, cooler air and soil temperatures during the day, and colder air temperatures at night (Forman and Baudry 1984).

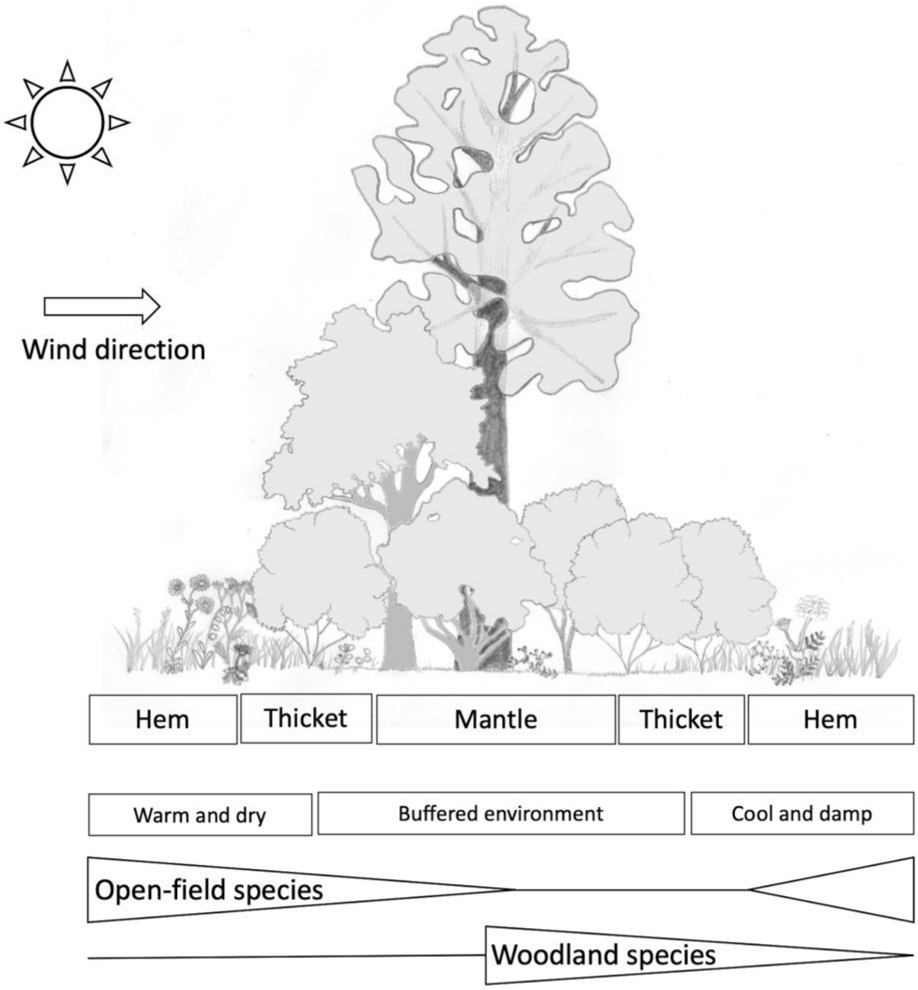

Figure 1: Schematic representation of a good-quality hedgerow with the three types of vegetation formations (herbaceous hem, shrubby thicket, and woody mantle) and the zonation pattern relating to the microclimatic alterations exerted by the hedgerow on its immediate environment.

These factors are locally modified, over twice the height of the hedgerow upwind and six to eight times its height leeward. Evaporation and windspeed are reduced on both sides of the hedgerow, but much of the effect takes place leeward, up to 16 and 28 times the height of the hedgerow for the two variables, respectively (Forman and Baudry 1984). Studies on windbreaks (hedgerows with high tree species designed to protect fields and orchards from wind) show that hedgerows of sufficient height can create a microclimate on the leeward side that is isolated from the atmosphere above, thus preventing wind damage to buds, flowers, and fruits, while reducing plant evapotranspiration and even protecting plants from frost (Norton 1988; Brandle et al. 2004; Smith et al. 2021). When trees are present, the centre of the hedgerow experiences the most buffered conditions, with high soil and air moisture along with cooler temperatures, very close to the conditions under a forest canopy (Vanneste, Govaert, Spicher, et al. 2020).

2.3 Synergism between structural vegetation heterogeneity and microclimate enhances microhabitat diversity

The repartition of plant species follows the microclimatic heterogeneity. Of the 36 plant species recorded in a hedgerow in western France, Forman and Baudry (1984) found that only one-quarter grew on both sides of the hedge. Open field species are mostly found upwind on the sunny side of the hedgerow, while mosses and forest species mainly occur in the centre of wide hedgerows with tree cover as well as on the leeward side (Figure 1). The hem on the sunny side of the hedgerow usually displays a higher diversity of herbaceous species than the shady side (Forman and Baudry 1984). Local microclimatic heterogeneity structures hedgerow plant communities, resulting in a zonation pattern (Figure 1).

In turn, plant communities play a role in structuring soil microhabitats and controlling the variability of soil surface properties that influence water infiltration, storage, and drainage as well as mineralisation or nutrient availability (Sitzia et al. 2014). By slowing down soil erosion in agricultural landscapes (Kort et al. 1998; Salvador-Blanes et al. 2006; Cullum et al. 2007; Sitzia et al. 2014), hedgerows vegetation prevents the removal of the clay particles forming the topsoil. The abundance of clay particles beneath and near the hedgerows increases the water-holding capacity of the soil (Kort et al. 1998; Holden et al. 2019). Moreover, hedgerow trees increase the formation of litter and the levels of humification (Sitzia et al. 2014). Soils in hedgerows typically accumulate organic matter compared to field soils (Forman and Baudry 1984; Agus et al. 1997; Kort et al. 1998; Isaac et al. 2003; Lin et al. 2009; Sitzia et al. 2014; Holden et al. 2019), making them good candidates for stocking organic carbon in soils (Van Vooren et al. 2017; Holden et al. 2019). As a result of both processes, soils in hedgerows present more micropores in addition to lower density and lower surface compaction (Holden et al. 2019), properties that enhance soil biodiversity. They also display higher nutrient-holding capacity than soils in adjacent fields (Lin et al. 2009; Holden et al. 2019), thus increasing their fertility.

In hedgerows, the structural heterogeneity of the vegetation therefore interacts with the microclimatic heterogeneity. For hedgerows of sufficient age and complexity, a synergy can thus develop as a result of this interaction, resulting in an increase in microhabitat diversity.

2.4 Hedgerows as ecotones

Mature hedgerows are characterized by a high microhabitat diversity, resulting from the interaction between structural vegetation heterogeneity and microclimatic heterogeneity. As such, one can refer to them as ecotones. Ecotones, namely transition areas between two or more habitat types, are notorious for harbouring very diverse biological communities (Kark 2017). Hedgerows represent an ecotone between three of the main terrestrial habitats: the hem relates to open habitats such as grasslands, meadows, and open fields, the thicket to semi-open habitats such as shrublands, and the mantle to forest habitats. Hedgerows will thus bring together species associated with each of these habitats (typical grassland species such as *Galium verum* L., *Anthyllis vulneraria* L., *Knautia arvensis* (L.) Coult., or typical forest species such as *Hyacinthoides non-scripta* (L.) Rothm. or *Lamium galeobdolon* (L.) L.), species preferring complex habitats such as forest edge species (Forman and Baudry 1984), and species that thrive due to the unique mosaic of microhabitats created by the structural complexity of hedgerows (Reading and Jofré 2009; Wolton et al. 2013; Medlock et al. 2020). An example of this synergistic effect is given by two forest plant species, *Poa nemoralis* L.

and *Geum urbanum* L., which have better reproductive success in hedgerows than in their original forest habitat (Vanneste, Van Den Berge, et al. 2020).

3. The positive effects of hedgerows on spontaneous biodiversity

Many studies have reported the positive effect of hedgerows on the diversity or abundance of various taxa (Table 1). Forman and Baudry (1984) note that a large proportion of the English countryside fauna can be observed in hedgerows at one time or another, while Pollard and Holland (2006) emphasise the status of hedgerows as one of the most important non-crop habitats for farmland arthropods. In this section, we aim at exploring the positive effects of hedgerows on spontaneous biodiversity at different spatial scales.

Taxa	Studies	A/B/R
Myriapods	Stašiov et al. 2017	R
Harvestmen	Stašiov et al. 2020	R
Predatory mites	Tuovinen 1994	A
Spiders	Duelli et al. 1990	R
	Maudsley et al. 2002	B
	Garratt et al. 2017	A
	Lefebvre et al. 2017	B
	Peñalver-Cruz et al. 2020	B
Moths	Merckx et al. 2010	A
	Merckx et al. 2012	R
Psyllids	Sotherton et al. 1981	A
Ladybirds	Long et al. 1998	B
	Burgio et al. 2004	R
	Puech et al. 2015	R
Carabid beetles	Burel 1989	R
	Duelli et al. 1990	R
	Charrier et al. 1997	B
	Long et al. 1998	B
	Maudsley et al. 2002	B
	Holland et al. 2009	B
	Puech et al. 2015	R
	Lefebvre et al. 2017	B
Staphylinid beetles	Maudsley et al. 2002	B
	Griffiths et al. 2007	R
	Holland et al. 2009	B
Syrphid flies	Long et al. 1998	B
	Alignier et al. 2014	A
	Haenke et al. 2014	A
	Inclán et al. 2016	B
	Garratt et al. 2017	A

Taxa	Studies	A/B/R
Butterflies	Dainese et al. 2015	R
Tachinid flies	Morandin and Kremen 2013	AR
	Dainese et al. 2015	R
	Inclán et al. 2016	B
Mirid bugs	Forman and Baudry 1984	R
Lacewings	Long et al. 1998	B
Wild bees and bumblebees	Hannon and Sisk 2009	R
	Cranmer et al. 2012	A
	Garratt et al. 2017	A
Tenthredinid wasps	Sotherton et al. 1981	A
Parasitoid wasps	Maier 1981	A
	Long et al. 1998	B
	Langer 2001	B
	Bianchi and Van Der Werf 2003	B
	Gagic et al. 2011	B
	Morandin et al. 2014	R
	Dainese et al. 2015	R
	Puech et al. 2015	R
	Inclán et al. 2016	B
Snails	Cameron et al. 1980	R
Newts	Joly et al. 2001	A
Birds	Wegner and Merriam 1979	B
	Hinsley and Bellamy 2000	R
	Batáry et al. 2010	R
Rodents	Pollard and Relton 1970	B
	Eldridge 1971	B
	Wegner and Merriam 1979	B
Bats	Entwistle 1996	B
	Verboom and Huitema 1997	B
	Boughey et al. 2011	R

Table 1: List of taxa for which the beneficial effect of hedgerows has been reported in the literature. Column A/B/R indicates to whether the studies are concerned with the abundance (A) or the species richness (R) of taxonomic groups present in hedgerows, or both (B).

3.1 Microhabitat diversity in hedgerows leads to high local species richness

Faunal studies have demonstrated that the high species diversity in hedgerows is a direct consequence of their microhabitat heterogeneity (Silva and Prince 2008; Le Viol et al. 2008; Fischer et al. 2013). Small-scale heterogeneity is known to promote biodiversity (Lawton et al. 2010). Such levels of microheterogeneity explain why alpha-biodiversity (species richness in a given community) is usually high in hedgerows and also why hedgerow abundance at the landscape scale leads to high levels of beta-diversity (dissimilarity between communities) and phenotypically diverse communities (Ponisio et al. 2016). High levels of beta-diversity between hedgerow habitats also hint at how different hedgerows can be in terms of the organisms that live in them (and thus in terms of interaction networks). It is therefore likely that the positive effect of hedgerows on spontaneous biodiversity is strong at small spatial scales (a few times the width of the hedgerow at most). This is corroborated by studies such as Maudsley et al. (2002), who showed that abundance and diversity of overwintering predatory arthropods in hedgerows was highly variable between micro-sites.

3.2 Hedgerows can serve as ecological corridors.

Hedgerows also influence spontaneous biodiversity at larger scales. For example, hedgerows have long been thought to act as ecological corridors (Harris and Gallaher 1989; Dover and Settele 2009) and enhance landscape connectivity between natural and semi-natural habitats (Forman and Baudry 1984). The presence of physically connected and rich semi-natural habitats such as hedgerows can indeed increase landscape permeability for many insect species (Cranmer 2004). Although the concept of ecological corridors does not apply to all species in the same way (Pe'er et al. 2005; Downs and Racey 2006), many studies have now ascertained that hedgerows increase animal and plant movements at the landscape scale (reviewed by Gilbert-Norton et al. 2010). In this respect, there is evidence for carabid beetles (Burel 1989), butterflies, bumblebees and other pollinators (Cranmer et al. 2012), newts (Joly et al. 2001), birds (Macclintock et al. 1977; Wegner and Merriam 1979), rodents (Pollard and Relton 1970; Eldridge 1971), and bats (Entwistle 1996; Verboom and Huitema 1997; Boughey et al. 2011). Nevertheless, dispersal may not always be continuous alongside hedgerows, while hedgerows themselves may not always be continuous. In this case, they may provide successive patches of favourable habitat that will act as a stepping stone and nonetheless favour dispersal (Slade et al. 2013). Higher levels of landscape connectivity due to hedgerows can increase wild flower pollination. Cranmer (2004) showed that the number of pollinator visits and seeds yielded in patches of *Salvia pratensis* L. linked to hedgerows was higher than in isolated patches.

3.3 Hedgerows increase species persistence at the landscape scale

3.3.1 Case study: hedgerows are crucial for the preservation of forest species in open field landscapes

Hedgerows are of particular importance as corridor and stepping-stone habitats for forest species. Large hedgerows with well-developed mantles and dense herbaceous layers represent favourable habitats for woodland species of insect, snails, birds, mammals, and plants (Williamson 1969; Pollard et al. 1974; Cameron et al. 1980; Forman and Baudry 1984; Burel and Baudry 1995; Charrier et al. 1997; McCollin et al. 2000; Sitzia 2007). Hedgerows house many forest-core species of plants (Pollard et al. 1974), while forest-edge species thrive in hedgerow thickets (Helliwell 1975). At the scale of Western Europe, Vanneste, Govaert, De Kesel, et al. (2020) showed that 55% of forest flora was also found in hedgerow habitats. Hedgerows had 11% less habitat-specialist species and 14% more habitat-generalist species compared to forests, with high levels of species turnover. In fact, only the most sciaphilous and dispersal-limited species from ancient forests are unable to grow in hedgerows due to their narrow ecological niche (Bailey 2007; Vanneste, Govaert, De Kesel, et al. 2020). Carabid beetle assemblages in hedgerows share many characteristics with those of woodland assemblages, especially the abundance of nocturnal predators and ground-dwelling shade-preferring species that prefer dense vegetation (Pollard 1971). Forman and Baudry (1984) reported that four-fifths of English forest bird species also nested in hedgerows. Pollard and Relton (1970) showed that hedgerows provided cover for woodland rodents. In agricultural landscapes, where there are few forest habitats, hedgerows can therefore play a key role regarding the persistence of forest species.

3.3.2 From local increase in species richness to increased species persistence at the landscape scale.

The importance of hedgerows for the preservation of forest species in agricultural landscapes illustrates well one of the impacts of hedgerows on spontaneous biodiversity. The diversity of micro-habitats increases species richness locally (high alpha diversity), but the presence of hedgerows is no guarantee that all micro-habitats are abundant at the landscape scale. Therefore, hedgerows do not necessarily increase the abundance of all organisms at the landscape scale. Indeed, among the publications listed in Table 1 that show the importance of hedgerows for different groups of organisms, 41% of the publications report a positive effect of hedgerows on the species richness within the groups considered. Only 24% of them reported a positive effect on the abundance of these organisms. The remaining 36% did not distinguish between the effects of hedgerows on abundance and diversity (the sum of the percentages is greater than one because one of the studies showed a joint effect on the species richness and abundance of tachinid flies).

It is therefore possible that the local increase in species richness due to micro-habitat diversity translates at the landscape scale into an increase in the probability of persistence of species that are specialists of these micro-habitats (such as forest species in the previous example). In other words, the presence of sufficient hedgerows in the landscape could ensure that many species will find some micro-habitat that suit them but not that these species will be much more abundant.

3.4 Does the positive impact of hedgerows on spontaneous biodiversity translate into a positive impact on functional biodiversity?

This section has demonstrated that hedgerows have undeniable positive impacts on spontaneous biodiversity. But can we benefit from these impacts from an agroecological point of view? Or more accurately, does the increase in species richness and species persistence translate into an increase in functional biodiversity susceptible to foster regulation services (pest control and pollination) in adjacent crops? Given that there is often a positive relationship between species richness and functional diversity (Biswas and Mallik 2011; Song et al. 2014), one could expect hedgerows to also increase functional biodiversity and associated biodiversity (biodiversity in action in crops). In the next section, we endeavor to elucidate the possible relations between hedgerow ecological functioning for agriculture and associated biodiversity in terms of pest and weed control and pollination.

This relationship is however not necessarily straightforward. We already showed that hedgerows increase the abundance of some taxa but not others. Hedgerows are likely to have a strong functional impact if they increase the abundance of those few key species that play major roles in the provision of ecosystem services (Mahaut et al. 2020). Moreover, the functional traits that allow some species to thrive in hedgerows may be very different from those that characterize species in crops, leading to different communities between fields and hedgerows. The positive effect of hedges on the most functionally important species could also be limited to periods when the regulating service cannot take place (outside of the flowering period of the crop or too late for pest regulation to take place). It could be spatially limited too, due to hedgerows heterogeneity or discontinuity. Finally, some characteristics of the hedgerows (age, length, management practices...) could alter the relationship between hedgerow spontaneous and associated biodiversity.

4. Hedgerows have the potential to foster some biotic regulation services

Here, we focus on two biotic regulation services, namely pollination along with pest and weed regulation in an agricultural context. Other regulation services provided by hedgerows, such as the reduction of soil erosion (Wu et al. 2010; Fan et al. 2015) or the control of residues of plant protection products (van de Zande et al. 2004; Lemieux and Vézina 2011) will not be addressed here.

4.1 Hedgerows host crop pests, natural enemies and pollinators

Hedgerows provide food resources and shelter to many animal taxa. Here we analyse how some can pose threats to crops (pests and pathogens) while others can be considered natural enemies (organisms that feed on pests, Wilby and Thomas 2002) or pollinators.

4.1.1 Hedgerows increase pollinator diversity but not their abundance

Hedgerows that offer both suitable nesting sites and large amounts of pollen and nectar resources throughout the year represent favourable habitats for pollinators (Bugg et al. 1998) (Simon et al. 2009; Carvell et al. 2011; Garibaldi et al. 2014; Schüepp et al. 2014; Kremen and M'Gonigle 2015; Schellhorn et al. 2015; M'Gonigle et al. 2017). Such hedgerows play host to a high diversity of pollinators, especially due to the presence of forest species (Croxton et al. 2005) and the role played by hedgerows as dispersal corridors and stepping stones (Cranmer et al. 2012; Slade et al. 2013). The main groups of pollinators in hedgerows include native bees (Corbit et al. 1999; Hannon and Sisk 2009), bumblebees (Garratt et al. 2017), syrphid flies (Long et al. 1998; Burgio et al. 2004), and many other Diptera families (Staley et al. 2019).

According to Carvell et al. (2011), hedgerows increase pollinator diversity rather than pollinator abundance, which rather depends on the abundance of floral resources. Several studies, which report that hedgerow restoration in agricultural landscape leads to increased levels of pollinator diversity, reach similar conclusions (Hannon and Sisk 2009; M'Gonigle et al. 2015; Sardiñas and Kremen 2015). Hedgerows seem to be more beneficial to generalist pollinators than to specialist species (Kleijn et al. 2015; Ponisio et al. 2017), although the conservation of specific plant species or the protection of mature hedgerows can favour specialist pollinator species (Kremen and M'Gonigle 2015; Ponisio et al. 2016; M'Gonigle et al. 2017; Kremen et al. 2018).

4.1.2 Natural enemies are diverse and possibly abundant in hedgerows

Communities of natural enemies are usually rather diverse in hedgerows (Sotherton et al. 1981; Paoletti et al. 1997; Amy 2015). Depending on whether they forage on the ground or in the vegetation canopy, they are split into three guilds. The guild of ground-active natural enemies forages in the litter and topsoil and includes some carabid and staphylinid beetles, lycosid spiders, ants, earwigs, and centipedes (Mathews et al. 2004). The guild of canopy-active natural enemies also features some carabid and staphylinid beetles along with coccinellid beetles, lacewings, earwigs, predatory bugs, hoverflies larvae, linyphiid spiders, and predatory mites. The third guild corresponds to parasitoid insects such as tachinid flies and parasitoid wasps and flies.

The diversity and abundance of natural enemies depends on hedgerow quality and complexity (Puech et al. 2015; Stašiov et al. 2017). Diverse and complex herbaceous fringes are necessary to host diverse communities of anthocorid bugs (Pollard 1968a), mirid bugs (Forman and Baudry 1984), carabid beetles (Pollard 1968b; Maudsley et al. 2002) and syrphid flies, for which the herbaceous flora of the hem provides 80% of the necessary food resources (Garratt et al. 2017). The abundance of soil litter due to the presence of trees in the mantle increases the abundance and diversity of staphylinid beetles and lycosid spiders (Garratt et al. 2017). Natural enemies can also benefit from nectar and pollen resources in hedgerows. Non-crop floral resources increase the longevity and fecundity of many short-lived parasitoid wasps (Winkler et al. 2006; Géneau et al. 2012; Morandin et al. 2014). Some predatory arthropods such as ladybirds and lacewings also benefit from floral resources as alternative sources of energy (Long et al. 1998; Bianchi et al. 2006), although they appear to be less dependent on them than parasitoids (Morandin et al. 2014). Hedgerows also provide overwintering sites for many natural enemies, regardless of whether they live in the hedgerow itself or come from nearby fields and other habitats.

Hedgerows support diverse natural enemy communities and there seems to be a trend towards a positive relationship between hedgerows and the relative abundance of natural enemies. For example, Gareau et al. (2013) report a six times higher natural enemies to pest ratio near hedgerows compared to other types of field edges. Morandin et al. (2011) found similar results and emphasize the role of the shrub layer in increasing the abundance of natural enemies. Note however that few studies deal with the abundance of natural enemies (as a general functional group) in hedgerows.

4.1.3 Hedgerows host few pests

The high plant diversity in hedgerows supports a high diversity of phytophagous arthropods that feed on leaves, nectar, pollen, or sap (Rieux et al. 1999; Debras et al. 2002). Young shrub and tree shoots increase the abundance of herbivorous arthropods (Amy 2015). Old hedgerows that include trees seem to host abundant populations of psyllids (Sotherton et al. 1981). Aphids can sometimes be abundant in grasses in hems (Al Hassan et al. 2013) or find alternative hosts in hedgerow vegetation. For example, the cereal aphid *Sitobion avenae* (Fabricius 1775) was found to feed on willow and alfalfa in hedgerows (Langer 2001), while the black bean aphid (*Aphis fabae* Scopoli, 1763) overwinters on European spindle in hedgerows (Cammel et al. 1989). But although the total number of herbivorous and opophagous arthropods is high in hedgerows, the number of pest species that are actually of concern for crops seems to be rather low, especially compared to the abundance of putative natural enemies in hedgerows (Morandin et al. 2011; Gareau et al. 2013).

Regarding crop pathogens, hedgerows may also occasionally represent disease reservoirs. Indeed, some pathogens or their vectors spend part of their lifecycles in hedgerow vegetation. The most emblematic example involves wheat rust (*Puccinia graminis* Pers. 1794), a pathogenic fungus reproducing sexually on barberry shrubs and responsible for costly epidemics on winter wheat. Barberry shrubs used to be planted as enclosures around houses and properties in Northern Europe and North America until it emerged that their presence amplified rust epidemics. Their progressive removal during the 20th century allowed for a substantial reduction in the intensity of rust epidemic (Zadoks 2008). Similarly, in some regions, juniper shrubs, primary hosts to the fungal agent of pear rust (*Gymnosporangium sabinae* (Dicks.) Oerst. 1863), have been eliminated to limit epidemics in orchards (Lace 2017). Till now, there is however a limited number of examples of diseases shared by crops and hedgerows. More studies are needed to understand the role of hedgerows as reservoirs of crop diseases.

Hedgerows may therefore house putative crop pests. Caution should therefore be exercised when establishing hedgerows in the vicinity of crops. Nevertheless, hedgerows and surrounding crops have few pests in common in most cases. Moreover, the number and diversity of pests in hedgerows remains much lower than in other types of semi-natural habitats (Paoletti et al. 1997). Morandin et al. (2011) and Morandin et al. (2014) found more pests in common between grass field margins and crops than between hedgerows and crops. However, with the diversification of crops linked to the agroecological transition, it seems important to take into account this possible negative impact of hedgerows in these more diversified systems.

4.2 Hedgerows pose little threat as a weed reservoir

The major difference between weeds and hedgerow plants (mostly plants from the hem) is that the latter has little impact on the flora of nearby fields. Indeed, weeds are generally pioneer species or species from perturbed environments that are susceptible to competition. They include many species of geophytes and therophytes. To the contrary, the vegetation of the hem is composed of competitive grassland species, including many perennial or biennial hemicryptophytic species (Jauzein 2011). Despite these differences, it is possible that a small number of hedgerow species, especially nitrophilous species, disperse into adjacent fields. For example, Boutin et al. (2001) showed that wet-habitat weed species found in the central position of hedgerows (e.g., *Lythrum salicaria* L., *Equisetum arvense* L., *Cicuta maculata* L.) can colonise nearby fields. Nevertheless, such examples remain relatively rare. However, Dainese et al. (2017) showed no effect of hedgerow cover on weed richness or cover. The relation between hedgerows and weeds thus remains uncertain.

4.3 Focus on some characteristics of hedgerows that foster functional diversity

The previous section already hinted at the fact that certain functional characteristics of hedgerows influence the presence of certain functional groups of pollinators, pests and natural enemies. In this section we elaborate on several mechanisms that link the functional ecological characteristics of hedgerows and the presence of these organisms.

4.3.1 Importance of the diversity of vegetation layers and spatial hedgerow characteristics

The diversity of vegetation layers (Constant et al. 1976; Ricou and Lecomte 1976) and their botanical complexity (Johnson and Beck 1988; Hinsley and Bellamy 2000) have been shown to determine the diversity of many taxonomic groups in hedgerows. The destruction of herbaceous vegetation in the hem and thicket due to overgrazing has proven detrimental for arthropods that use it for shelter and foraging (Johnson and Beck 1988). The presence of a tree layer plays a central role in the sheltering of diverse communities. Hedgerow trees provide rare shelter for adult moths in agricultural landscapes, leading to a local increase in their diversity (Merckx et al. 2010; Merckx et al. 2012). The shrub and tree layers create litter over the soil, leading to more fertile soils (Lin et al. 2009; Holden et al. 2019) and richer soil communities than those in surrounding agricultural soils (Duran Zuazo and Rodriguez Pleguezuelo 2008). Fungal biomass increases in hedgerow soils (Monokrousos et al. 2006), which present very distinct fungal and mycorrhiza communities (Holden et al. 2019). Earthworms are also more abundant in hedgerow soils than in field soils, although they are still less abundant than in pasture soils (Hansen et al. 1989; Holden et al. 2019).

The spatial characteristics of hedgerows such as their length, width, height, and continuity in relation to hedgerow management are also important factors impacting biodiversity. The taxonomic diversity of harvestman (Stašiov et al. 2020), birds, and mammals (Johnson and Beck 1988) increases with hedgerow length, while the diversity of nesting birds increases with hedgerow height (Hinsley and Bellamy 2000). The abundance of herbivores and predators was found to be determined by foliage density, while the abundance of detritivore arthropods and linyphiid spiders was negatively affected by hedgerow discontinuity (Amy 2015).

4.3.2 An example of spatial niche segregation: diversity of vegetation layers and arthropod overwintering

Niche segregation can explain the diversity of natural enemies at overwintering sites in hedgerows (Figure 2). Canopy-active natural enemies display a rather horizontal segregation, occupying different botanical formations (Figure 2) and overwintering at different stages of their lifecycle. Adult ladybirds overwinter in the mantle in tree trunk crevasses, taking advantage of the thermal capacity of the bark warming in sunlight (Burgio et al. 2004). Some adult lacewings overwinter in the thicket underneath the marcescent leaves of some shrub species such as hawthorn or hornbeam, while some species also overwinter in mistletoe (Weihrauch 2008). Some syrphid flies overwinter in the hem as larvae in the stubbles and hollow stems of desiccated plants (widespread in the Apiaceae family). Many parasitoid wasps overwinter as eggs laid on the eggs of their hosts, which can be found on buds or marcescent leaves in the shrub or tree layer (Pollard et al. 1974; Corbett and Rosenheim 1996). Linyphiid spiders make use of herbaceous vegetation and marcescent leaves as shelter and hunting grounds for winter-active springtails (Sunderland et al. 1986; Vanin and Turchetto 2007). On the contrary, most ground-active natural enemies overwinter as adults and display a more vertical niche segregation. Lycosid spiders overwinter aboveground in litter and herbaceous vegetation (Maudsley et al. 2002). Carabid beetles overwinter in litter and topsoil, mostly between 0 and 10 cm belowground (Desender 1982; Maudsley et al. 2002). Moreover, the deeper the litter, the larger the carabid species encountered: there is also horizontal niche segregation among carabid beetles, with small species being more abundant in the hems and large species in the mantles (Figure 2; Desender 1982). Staphylinid beetles overwinter deeper in the soil, mostly between 10 and 20 cm belowground (Maudsley et al. 2002).

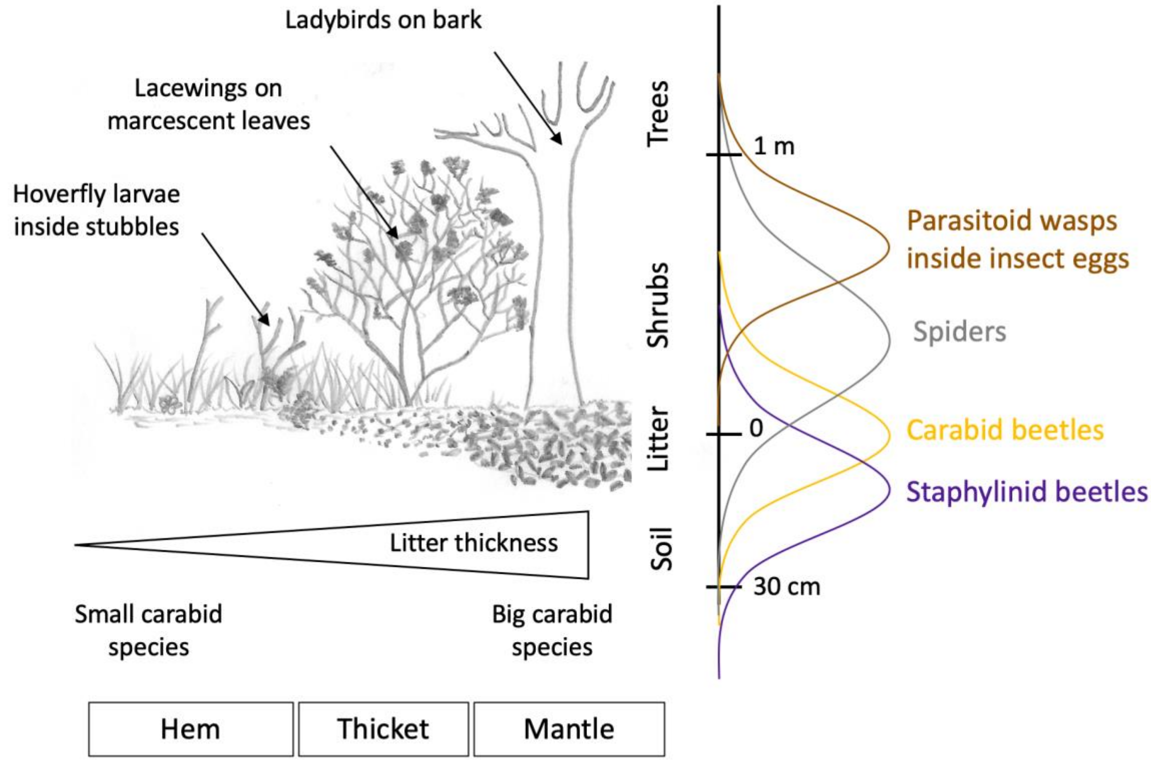

Figure 2: Niche segregation of natural enemies at overwintering sites in hedgerows. Inspired by Pollard et al. 1974; Desender et al. 1982; Sunderland et al. 1986; Corbett and Rosenheim 1996; Maudsley et al. 2002; Burgio et al. 2004; Weihrauch 2008.

4.3.3 Importance of the temporal complementarity of nectar resources in hedgerows throughout the year

Nectar resources particularly depend on the diversity of herbaceous species in the hem and the blooming period of different shrub and tree species (Bugg et al. 1998; Simon et al. 2009; Garibaldi et al. 2014; Haenke et al. 2014; Schüepp et al. 2014). Functional plant species diversity can support year-round pollination if the species have different flowering periods, thereby providing nectar resources to insects from diapause emergence in spring to pre-diapause resource gathering in autumn (Bugg et al. 1998; Simon et al. 2009). Rebulard (2018) provides an example of such ecological complementarity in European hedgerows, considering only native tree and shrub species. Winter-flowering species such as *Salix caprea* L., *Hedera helix* L. and *Prunus spinosa* L. provide nectar and pollen early in the season. They are followed by spring-flowering species such as *Sambucus nigra* L., *Crataegus monogyna* Jacq. or *Prunus avium* L. In summer, resources are provided by *Tilia cordata* Mill. or *Rosa* spp. and in autumn by *Rubus* spp. L. or *Hedera helix* L. Other examples can be found in Bugg et al. (1998) and Simon et al. (2009).

Owing to the correspondence between the plant flowering time and the time of imago emergence, different groups of pollinators will feed on different plant species over time. Dung flies and syrphid flies that have overwintered as adults feed preferentially on blackthorn in spring; solitary bees, bumblebees, and syrphid flies feed on hawthorn in late spring and brambles in summer; and muscid, tachinid, and calliphorid flies feed on ivy in autumn (Staley et al. 2019).

4.3.4 Importance of some particular species in hedgerow ecosystems

The taxonomic composition of hedgerows may also be a key factor regarding the composition of hedgerow communities. Some shrub and tree species are of particular interest regarding hedgerow biodiversity. For example, Constant et al. (1976) noted that in England, oak-dominated hedgerows house twice as many nesting bird species as coniferous hedgerows, while Pollard et al. (1974) showed that oak and hawthorn hedges support the most diverse insect fauna in England. Oaks and limes appear to host high densities of predatory mites (Tuovinen 1994). Some tree (blackthorn, common spindle) and weed species (wild teasel, red-root amaranth, wild carrot, ...) are important for providing food and shelter to coccinellid beetles once crops are harvested (Burgio et al. 2004). Ivy is also an important source of nectar for wasps in autumn (Jacobs et al. 2010) and an important overwintering habitat for lacewings (Weihrauch 2008).

Pest exchange between hedgerows and crops becomes more likely when hedgerows play host to wild plants of the same family as the crop. Examples can be found in orchards. Many trees in the family Rosaceae are grown in orchards (e.g., pear tree, apple tree, cherry tree, plum tree), while many hedgerow shrubs (e.g., blackthorn, hawthorn, brambles, dog roses) and trees (e.g., wild cherry, bird cherry, medlar tree, European crab apple) belong to the same family. Cultivated and wild woody species of this family share pests, which could accumulate in hedgerows and spill over into the adjacent orchards (Peñalver-Cruz et al. 2020). Overall, however, pest species found in hedgerows only rarely attack crops, unless pests find secondary hosts among the hedgerow flora. Similar results have been found for other semi-natural habitats, especially field margins (Denys and Tscharntke 2002; Marshall 2004).

4.4 Anthropogenic disturbances impact hedgerow functional biodiversity

Hedgerows can be planted, managed or cut by humans, and are part of a landscape matrix dominated by human activities. While the effects of such transformations on hedgerow biodiversity are partially known, little is known about their impact on functional hedgerow biodiversity. In this section, we focus on two such transformations: hedgerow management and adjacent crops and agricultural practices.

Since many hedgerow characteristics (length, hight, density, age, species composition, structural complexity...) can be altered by human management, hedgerow management often has a strong impact on hedgerow communities. Hedgerow trimming promotes shoot growth and thus the density of herbivorous insects in hedgerows (Sotherton et al. 1981). Moreover, annual hedgerow cutting tends to reduce the number of flowers and the biomass of the fruits produced, which is unfavourable for nectar-feeding arthropods and fruit-eating birds. In comparison, hedgerow cutting every three years leads to increased flower and berry production (Staley et al. 2012). Decreasing the frequency of hedgerow trimming also improves the diversity of butterfly assemblages (Staley et al. 2016). The presence of trees of different ages favours saproxylic insect communities (Clements and Alexander 2009) and reduces the abundance of herbivorous insects, which are less abundant in mature trees (Sotherton et al. 1981). Regular trimming of the thicket every few years and the presence of trees of different ages thus appears favourable to functional biodiversity. Nevertheless, this effect is likely to change with hedgerow age and species composition. Newly planted hedges have functional characteristics that are close to the sum of those of the planted species. Over time, the species composition of the hedgerow undergoes a natural evolution that transforms its functional characteristics. Hedgerows are first colonised by species with high dispersal capabilities (Closset-Kopp et al. 2016): epizoochorous dispersal and reproduction by seeds are associated with rapid colonisation and are characteristic of many plant species found in young hedgerows (Litza and Diekmann 2019). Species with low dispersal capabilities colonise hedgerows over much longer periods, thus stressing the importance of protecting ancient hedgerows (Closset-Kopp et al. 2017). Therefore, as in forest habitats, hedgerow age is correlated with hedgerow diversity (Litza and Diekmann 2019). Older hedgerows are therefore richer in biodiversity, but in terms of functional diversity, the species initially planted may have disappeared due to competition and the functional properties of the hedgerows will have likely changed. In addition, older hedgerows, potentially taller and wider, are also more difficult to manage.

Adjacent crops and agricultural practices such as the use of fertilisers or pesticides can also modify hedgerow animal and plant communities (Robinson and Sutherland 2002; Petit et al. 2003). Intensive management of adjacent land is particularly detrimental to forest species living in hedgerows (Closset-Kopp et al. 2016; Closset-Kopp et al. 2017; Lenoir et al. 2019); Although many human management practices appear hazardous for hedgerow biodiversity, some data suggest that hedgerows are actually quite resilient to anthropogenic disturbances. Staley et al. (2013) reported changes in hedgerow diversity over the past 70 years. They identified a decrease in beta-diversity due to taxonomic homogenisation and a shift towards more nitrophilous flora, two phenomena that are significant in all natural and semi-natural habitats (Olden and Rooney 2006; Critchley et al. 2013). However, they also showed an increase in alpha-diversity of English hedgerows over time, suggesting that the introduction of exotic species and the development of higher soil fertility species did not result in the local extinction of many of the original species. Furthermore, they highlighted that the changes in hedgerow quality and plant diversity were not directly linked to the increase in land-use intensification in the surrounding landscape, indicating some levels of resilience in hedgerow plant communities to anthropogenic disturbances in terms of biodiversity.

To sum up section 4, hedgerows harbor diverse communities of pollinators and putative natural enemies while hosting few potential pests. The boundaries between these broad functional groups are not clear-cut. Some carabid beetles are predators at the larval stage but grain eaters at the imaginal stage. They can thus change from natural enemies to pests if they eat crop seeds, or remain beneficial organisms if they consume weed seeds and participate to the regulation of weed seedbanks (Carbonne et al. 2020).

Hedgerows thus have thus the potential to promote pest regulation and pollination in neighbouring fields. However, as pointed out by Karp et al. (2018) the presence of beneficial organisms does not guarantee the provision of regulation and pollination services, which involve complex ecological functions that occur at specific times and places. In the following section we analyse whether the positive effects of hedgerows on pollinators and natural enemies translates into actual biocontrol and pollination services.

5. Hedgerows can provide pest regulation and pollination services in agriculture but only in specific conditions

5.1. Pollinators and natural enemies, but also pests, spill over into neighbouring fields

A concern of farmers with the plantation of hedgerows is the spillover of crop pests from hedgerows into neighbouring fields (Brodt et al. 2009). However, the evidence for such dispersal is scarce. Aside from the examples of wheat rust and pear rust cited above (Zadoks 2008; Lace 2017), the main evidence concerns aphids. Some wild tree species host overwintering crop aphids, which can disperse back towards the crop in spring (Langer 2001). Alignier et al. (2014) found that the proximity of wood cover increased the risk of the early colonisation of cereals by aphids. Otherwise, the majority of examples from the literature concern tropical agroforestry, where the crops are often tree species that share pest species with the surrounding hedgerows (reviewed by Schroth et al. 2000). Therefore, it appears that in temperate agricultural landscapes, hedgerows may increase the pressure of pests in the surrounding fields but that this risk seems limited to certain pest taxa. More knowledge about this potentially negative effect of hedgerows is needed. The spillover of pests from other types of semi-natural habitats such as flower strips and weed field margins has also been documented (Al Hassan et al. 2013).

Contrary to pests, the spillover of natural enemies and pollinators from hedgerows has been widely documented (Bianchi et al. 2006; Griffiths et al. 2007; Dainese et al. 2017; Lefebvre et al. 2017; Albrecht et al. 2020), making hedgerows desirable semi-natural habitats in agri-environmental schemes (Kleijn et al. 2006) (Batáry et al. 2010). Among natural enemies and pollinators, spillover has been documented for many taxa (Table 2).

Natural enemies and pollinators leaving hedgerows for adjacent fields tend to stay within a few dozen meters from the hedgerows. Gareau et al. (2013) found a high natural enemy to pest ratio in hedgerows but showed that this beneficial ratio disappeared less than 50 m into the fields. Table 2 reports 11 studies illustrating that the diversity of beneficial organisms dispersing from hedgerows to adjacent crops decreases with the distance to the crop. Most studies report that hedgerows do not have impact on the communities of beneficial arthropods beyond 200 m into the fields. Notable exceptions are values extrapolated from Garratt et al. (2017) regarding linyphiid spiders, staphylinid beetles, and aphids, while parasitoid wasps appear to disperse to any distance from the hedgerows (Table 2). These results may be attributable to the dispersal modes and abilities of the different taxa under consideration. Aphids (in their alate stage) and parasitoid wasps are minute insects that are passively dispersed by the wind and eventually intercepted by hedgerows (Roschewitz et al. 2005a), while linyphiid spiders and flying staphylinid beetles are also windborne and can disperse further than lycosid spiders and carabid beetles, which are mainly ground-dwelling organisms. Nevertheless, pollinators, which are all flying insects, do not appear to disperse further than 200 meters into the fields (Garratt et al. 2017). Holland et al. (2009) showed that the effects of post-overwintering dispersal from hedgerows tend to disappear in summer, except in close proximity to hedgerows. Albrecht et al. (2020) demonstrated that both pollination and pest control imputed to the spillover of beneficial arthropods decreased exponentially from the centre of semi-natural habitats (hedgerows or flower strips). These results suggest that the spillover of beneficial arthropods from hedgerows to adjacent fields does occur but could remain limited to the proximity of the hedgerows. This highlights the importance of the spatial arrangement of hedgerows in the landscape in order to increase biotic regulation services in crops.

Study	Organisms	Results	Distance
Tuovinen (1994)	Predatory mites	Spillover from hedgerows into adjacent fields	No data
Varchola and Dunn (2001)	Carabid beetles		
Debras et al. (2007)	Earwings		
Haenke et al. (2014)	Syrphid flies		
Dainese et al. (2015)	Tachinid flies		
Puech et al. (2015)	Parasitoid wasps		
Dainese et al. (2017)	Parasitoid wasps		
	Native bees		
	Syrphid flies		
	Butterflies		
Langer (2001)	Parasitoid wasps	Spillover from short rotation coppice hedgerows into adjacent barley field	20 m
Földesi and Kovács-Hostyánszki (2014)	Syrphid flies	Spillover from hedgerows into adjacent fields	20 m
Pollard 1972	Syrphid flies	Woodland species living in hedgerows and laying eggs into adjacent crops	30 m
Inclán et al. (2016)	Tachinid flies	Spillover from hedgerows into adjacent fields	40 m
Long et al. (1998)	Ladybirds	Spillover from hedgerows into adjacent fields	80 m
	Lacewings		
	Syrphid flies		
	Parasitoid wasps		
Garratt et al. (2017)	Lycosid spiders	Spillover from hedgerows into adjacent fields	60 - 80 m
	Native bees		100 - 150 m
	Syrphid flies		150 - 200 m
Fournier and Loreau (1999)	Carabid beetles	Hedgerows favour the diversity of carabid beetles in adjacent fields	100 m
Morandin and Kremen (2013)	Native bees	Spillover from hedgerows into adjacent fields	100 m
Morandin et al. (2014)	Parasitoid wasps	Pest control	100 m
	Ladybirds		> 200 m
Alignier et al. (2014)	Parasitoid wasps	Higher aphid parasitism near hedgerows	500 m
Garratt et al. (2017)	Linyphiid spiders	Spillover from hedgerows into adjacent fields	400 - 500 m
	Staphylinid beetles		700 - 800 m
	Cereal aphids		800 - 900 m

Table 2: Studies demonstrating the spatial effect of hedgerows on the spillover of beneficial arthropods into adjacent crops. Some of the studies listed here provide quantitative data regarding the dispersal distance of natural enemies and pests from hedgerows.

5.2. Hedgerows provide biocontrol and pollination services to neighbouring fields but only in specific conditions

According to the "exporter hypothesis" (Morandin and Kremen 2013; Kremen et al. 2019; Albrecht et al. 2020), the spillover of beneficial arthropods from semi-natural habitats to adjacent fields should enhance pollination and biocontrol in these fields (Rusch et al. 2010; Pywell et al. 2015; Tschumi et al. 2015). Hedgerows should therefore contribute to providing adjacent crops with increased regulation services (Garibaldi et al. 2014; Schüepp et al. 2014; Dainese et al. 2015; Dainese et al. 2017; Garratt et al. 2017). However, many studies revealing the spillover of beneficial arthropods do not evaluate the consequences in terms of regulation services. Therefore, as pointed out by Griffiths et al. (2008), most studies demonstrate the potential for regulation rather than the actual regulation itself. Here we investigate the actual regulation services provided by hedgerows, focusing on pollination and pest biocontrol. We found several examples demonstrating increased biocontrol due to hedgerows. Many of them can be categorised into two groups: studies showing successful aphid regulation by parasitoids in annual crops (Alignier et al. 2014; Morandin et al. 2014), and studies demonstrating increased biocontrol in orchards surrounded by hedgerows (Debras et al. 2008; Ricci et al. 2011; Maalouly et al. 2013).

5.2.1. Successful aphid regulation by hedgerow parasitoid wasps in annual crops

We found two studies confirming the increased biocontrol of aphids by parasitoid wasps in the vicinity of hedgerows. Alignier et al. (2014) showed that aphid parasitism was higher close to hedgerows and up to 500 m into the investigated wheat fields. Morandin et al. (2014)

demonstrated that the parasitism of tomato aphids was higher up to 100 m into the fields. They reported that few of the fields surrounded by hedgerows reached the threshold of pests required for pesticide application (but attacks by aphids were quite limited during their study).

5.2.2. Successful cases of biocontrol in orchards surrounded by hedgerows

We found three studies demonstrating successful hedgerow-related biocontrol in orchards. Debras et al. (2008) highlighted that populations of psyllids attacking pear trees were reduced near hedgerows, probably due to the favourable microclimatic effect of hedgerows on natural enemies. Ricci et al. (2011) showed that the presence of hedgerows reduced the number of codling moth larvae on apple trees. Maalouly et al. (2013) showed that increased rates of parasitism of codling moth in organic orchards were correlated with the presence of hedgerows.

The above examples demonstrate that under certain conditions, the presence of hedgerows near the crops is associated with increased biocontrol. Nevertheless, the movement of beneficial organisms from hedgerows to fields, and thus their action, often occurs within a few dozens of metres from the hedgerow. Thus, landscapes composed of smaller fields with a low ratio of field area to hedge length should favour biocontrol processes. This is in line with Meehan et al. (2011) and Larsen and Noack (2020), who show that agricultural landscapes with smaller fields require less pesticide to regulate pests and are less variable from year to year than homogeneous landscapes with large fields. These results suggest that in small fields surrounded by semi-natural elements, including hedgerows, effective pest control may naturally occur.

5.2.3. Cases where spillover does not translate into enhanced biotic regulation services

In contrast to the successful examples listed above, we found other cases that failed to demonstrate increased pollination or pest control associated with the spillover of beneficial arthropods. In the cereal fields studied by Dainese et al. (2017), biocontrol by natural enemies was high but unrelated to the presence or complexity of hedgerows near the fields. Regarding pollinators, Sardiñas and Kremen (2015) found that neither the presence of hedgerows nor their distance impacted the pollination of sunflower crops, even though hedgerows support diverse pollinator communities. More recently, Albrecht et al. (2020) conducted a meta-analysis of the effectiveness of hedgerows to control pests and foster pollination. They revealed that interstudy variability is such that hedgerows cannot be considered to reliably increase pollination and biocontrol services in adjacent crops. Increased biocontrol and pollination due to hedgerows thus appears to be case-specific.

5.3. Regulation services supported by hedgerows depend on the characteristics of crops, hedgerows and beneficial organisms

Although hedgerows inconsistently provide regulation services to neighbouring fields, other types of semi-natural habitats or agroecological infrastructures have been reported to be more successful (Holland et al. 2017; Raderschall et al. 2021): for example, beetle banks (Collins et al. 2002), grass field margins (Rusch et al. 2010), and flower strips (Scheper et al. 2015; Tschumi et al. 2015; Kleijn et al. 2019; Albrecht et al. 2020). Moreover, exclusion experiments in the field provide numerous successful examples of biocontrol in crops (e.g., Schmidt et al. 2003; Rusch et al. 2013; Tamburini et al. 2016; Dainese et al. 2017). Therefore, how can we explain the difference between hedgerows and other semi-natural elements? For

Albrecht et al. (2020), hedgerows do not foster intensive regulation services because they are not designed for that purpose. Indeed, hedgerows are most of the time long-standing elements in agricultural landscapes and their composition is the result of the natural dispersion of species present in the surrounding natural habitats. In the contrary, flower strips specifically designed to foster the presence of a few natural enemies in order to keep a few target pests at bay successfully increase biocontrol.

The benefits conferred by hedgerows in terms of biocontrol and pollination depend on whether the high spontaneous biodiversity of hedgerows can boost associated biodiversity in nearby crops. Regulation services in crops may be provided by different biotic communities than those housed by hedgerows. Hedgerows could improve regulation services in crops only if some organisms belong to both communities or if the hedgerow community has a strong positive impact on the field community.

5.3.1. Differences in arthropod communities between cultivated crop fields and hedgerows

Arthropod communities in hedgerows and fields planted with annual crops seem to be rather distinct. Indeed, Sardiñas and Kremen (2015) and Dainese et al. (2015, 2017) demonstrated that, although pollination and pest control services are provided in crops flanked by hedgerows, hedgerows themselves contribute little to these services despite their high pollinator and natural enemy diversity. This points to differences in the communities that perform the same task in the two habitats. Moreover, Debras et al. (2006) highlighted that the presence of hedgerows explains only 2% of the variance in biocontrol measured in crops compared to 12% for agricultural practices and 30% for environmental variables. Langer (2001) showed that different species of parasitoid wasps attack aphids in different habitats. Many species in hedgerow communities are habitat-specialists. Paoletti et al. (1997) observed that 40-50% of arthropod species in hedgerows and grass field margins are specific to either habitat, compared to 20-40% in nearby fields. Griffiths et al. (2007) found that arthropod communities in hedgerows, field edges, and fence edges differed from one another, with fence edge communities, which include generalist predators and species with high dispersal capabilities, being closer to field communities. Communities in degraded hedgerows supported more unique species, species more vulnerable to habitat fragmentation, and species with low dispersal power. This evidence points to relatively separate communities in hedgerows and annual crop fields (but see Rand et al. 2006), although the degree of resemblance depends on both crop and hedgerow characteristics.

Crop and hedgerow communities may be characterised by different dispersal traits. Forman and Baudry (1984) indicate that carabid beetle communities in hedgerows include many forest species. The numerous nocturnal predators and ground-dwelling light-intolerant species requiring high vegetation cover are likely to move only a short distance into fields, contrary to open-country species found in grass field margins and beetle banks (Pollard 1971; Pollard et al. 1974; Collins et al. 2002). A similar limited dispersal of forest species in fields was found for syrphid flies (Forman and Baudry 1984). Duelli et al. (1990). Bugg et al. (1998) separate arthropod species into “hard-edge” and “soft-edge” species: the dispersal of the former is strongly impeded by changes in the type of vegetation in fields, field edges, and hedgerows, while the dispersal of the latter is not impacted by such changes. Duelli et al. (1990) showed that many hedgerow species are “hard-edge” species and thus unlikely to disperse into fields, while many field species are “soft-edge” species with high dispersal capabilities.

Finally, some studies suggest that the local biotic dynamics in crop fields are only marginally impacted by the immigration of organisms from outside the field. Vialatte et al. (2007) found a marked genetic difference between local (field) aphid populations and migrants on wheat. This suggest that immigration levels were of lower significance than local field dynamics during the cropping season.

5.3.2. Orchards and hedgerows have similar beneficial arthropod communities

Orchards represent a special case of crops in terms of interaction with hedgerows. Depending on the tree species planted, hedgerows and orchards may display rather similar communities of beneficial arthropods (Rieux et al. 1999; Debras et al. 2002; Maudsley et al. 2002; Miñarro and Dapena 2003; Debras et al. 2007; Boreau de Roincé et al. 2012; Miñarro and Prida 2013). Moreover, hedgerow and orchard vegetations have low levels of contrast. Both factors should thus facilitate movements of beneficial arthropods between hedgerows and orchards (Duelli et al. 1990; Rand et al. 2006; Schellhorn et al. 2014; Inclán et al. 2016). And indeed, high levels of arthropod movements have been recorded between the two habitats, either for foraging during the vegetation season (Debras et al. 2007; Moerkens et al. 2010; Lefebvre et al. 2017) or for overwintering (Sorribas et al. 2016; Peñalver-Cruz et al. 2020). These movements increase the abundance of beneficial arthropods and affect their distribution in orchards (Debras et al. 2008; Ricci et al. 2011), especially compared to isolated trees (Schüepp et al. 2014). According to the “exporter hypothesis”, these movements should result in higher levels of pest control (Debras et al. 2008; Ricci et al. 2011; Maalouly et al. 2013).

In this example, pollination and pest control are provided by mobile beneficial arthropods that belong to both the spontaneous biodiversity of hedgerows and the associated biodiversity of orchards.

5,3,3 Hedgerows ensure temporal continuity of resource availability for some beneficial arthropods

Several studies have demonstrated the positive impact of hedgerows on the rate of pest parasitism by parasitoid wasps in both orchards (Ricci et al. 2011; Maalouly et al. 2013) and annual crops (Alignier et al. 2014; Morandin et al. 2014). At the landscape scale, parasitoids usually form metapopulations driven by habitat fragmentation and dispersal (Rusch et al. 2010), which makes them highly sensitive to the proportion of suitable habitat and host density in the landscape (Hirzel et al. 2007). Dispersal between favourable habitats is usually not a limiting factor for parasitoid wasps. Given their small size, direct dispersal by these insects is very limited (Weisser and Völkl 1997), although they can, like their aphid hosts, disperse passively following wind gusts over several kilometres (Roschewitz et al. 2005a). Habitat quality may, however, be more problematic. Parasitoid wasps are highly dependent on flower nectar as an additional source of food (Maier 1981; Gagic et al. 2011; Puech et al. 2015). Indeed, nectar resources strongly increase the fitness of wasps in terms of survival (Lavandero I et al. 2006), longevity (Wäckers 2001; Géneau et al. 2012), fecundity (Tylianakis et al. 2004; Winkler et al. 2006), and parasitic efficacy (Baggen et al. 1999). The rareness of flower resources in agricultural landscapes combined with the massive positive effect of hedgerow flower resources on the fitness of parasitic wasps may explain why hedgerows often increase their abundance and parasitic activity.

Another example of the high benefit of hedgerows for crop-associated biodiversity is the presence of overwintering sites near crops. Many studies have demonstrated that the presence of overwintering sites in close proximity to crops allows for the early colonisation of the crop by natural enemies (Langer 2001; Varchola and Dunn 2001; Ponti et al. 2005; Alignier et al. 2014; Peñalver-Cruz et al. 2020). However, among these studies, only Alignier et al. (2014) demonstrate the positive effect of hedgerows on aphid biocontrol in early spring (and not afterwards). Here the positive impact of hedgerows is limited in time, and the local dynamics of field populations later in the season conceal the effect of the post-overwintering colonisation of the crop (Vialatte et al. 2007). Taking temporal aspects into account in biocontrol dynamics is essential to ensure that biocontrol agents have sufficient resources throughout the year (i.e., alternative prey and non-prey food resources, shelter, oversummering and/or overwintering habitats) in order to be present at the right time with respect to pest development (Le Gal et al. 2020; Iuliano and Gratton 2020).

5.4. Hedgerows contribute to landscape diversity, often enhancing regulation services

So far, we have examined the effects of hedgerows on pollination and pest regulation at the scale of the adjacent crop fields. However, just as hedgerows impact the movement of spontaneous flora, insects, birds, or bats at the landscape scale, they also have a positive impact on regulation services through increased landscape diversity or heterogeneity.

5.4.1. Hedgerows provide pollination and biocontrol services through landscape diversification

Depending on the characteristics of the plants and beneficial organisms involved, hedgerows promote pollination and biocontrol at the local scale (a few hundred metres at most). However, the provision of such regulation services also depends on the landscape context, broadly referred to as landscape complexity (Gurr et al. 2003; Tscharntke et al. 2007; Rusch et al. 2010). The complexity of agricultural landscapes is usually defined at the scale of a few square kilometres (Cranmer 2004; Rusch et al. 2013) and includes, among other variables, crop diversity, land-use heterogeneity, abundance of natural and semi-natural elements, field size, and landscape organisation and connectivity.

The positive effect of landscape heterogeneity on pollination and biocontrol leads to a greater abundance and diversity of resources and shelter for beneficial organisms. Pywell et al. (2006) showed that the richness of bumblebees, insects that feed almost exclusively on flower nectar, was positively correlated to the abundance and richness of eudicots and land-use heterogeneity. Similarly, Nicholls and Altieri (2013) highlighted that the greater abundance and diversity of weeds increased the abundance and diversity of bees in crop fields. Regarding biocontrol, Griffiths et al. (2008) showed that landscape heterogeneity contributed to greater invertebrate (prey) diversity, and therefore, the increased effectiveness of natural enemies. Östman et al. (2001) stressed that landscape complexity increased the presence of overwintering habitats for natural enemies, leading to a reduction in aphid populations by natural enemies early in the season during aphid establishment. Many other studies have successfully linked landscape complexity to regulation services (e.g., Roschewitz et al. 2005b; Rusch et al. 2010; Gagic et al. 2011; Chaplin-Kramer and Kremen 2012; Rusch et al. 2013; Dainese et al. 2017; Raderschall et al. 2021). Hedgerows play an important part in this landscape diversification. Bianchi et al. (2006) demonstrated that the effect of hedgerows on natural enemies and pollinators depends on the complexity of the landscape, revealing the beneficial or neutral effects of hedgerows on natural enemies and pest biocontrol in 85% of analysed studies. Schüepp et al. (2014) showed that pollinators visited flower crops more often in landscapes with high amounts of hedgerows and woody habitats. Finally, Dainese et al. (2017) found that high landscape-scale hedgerow cover increased aphid parasitism by 6%, increased pollinator visits to crops, and subsequently increased crop seed set by 70%.

5.4.2. Provision of regulation services by hedgerows depends on the landscape context

The examples presented in the previous sections show that hedgerows have a positive impact on regulation services when they provide ecological functions that are necessary for the beneficial organisms but not (or not enough) found in the surrounding fields. This is likely to occur in simplified landscapes with few resources and depleted beneficial populations. In complex landscapes, however, where resources are more abundant and accessible, hedgerows may have less of an effect on beneficial arthropods. Following Tscharntke et al. (2005) and Kleijn et al. (2011), the maximum effect of hedgerows and other semi-natural habitats occurs in landscapes of intermediate complexity, where landscape simplification is not too detrimental to beneficial organisms but where resources are sufficiently rare to make a difference (Thies et al. 2005; Batáry et al. 2011; Scheper et al. 2013; Scheper et al. 2015; Raderschall et al. 2021).

To date, intensive agricultural landscapes have been increasingly simplified and pests are mostly controlled with pesticides. But, pesticides not only may prove to be increasingly ineffective and environmentally detrimental, but in addition they may also impact non-target organisms (Iyaniwura 1991; Pelosi et al. 2014; Zaller and Brühl 2019) and thus impede ecological functioning in such treated agroecosystems (Stanley et al. 2015; Prashar and Shah 2016). This raises several questions. What are the impacts of pesticides on hedgerow communities and associated biocontrol in landscapes where some fields are sprayed with pesticides and some are not? What roles do hedgerows play within an intensification gradient ranging from intensive agricultural landscapes to pesticide-free agroecological landscapes (Bianchi et al. 2006; Chaplin-Kramer and Kremen 2012)? How can we better understand and take into account the impacts of human management on hedgerow-related biocontrol (Carvell et al. 2011; Dainese et al. 2017)?

Increasing functional biodiversity in complex agricultural landscapes can have synergistic effects with hedgerow-related regulation services. For example, more diverse communities of weeds and arthropods in crops may benefit more from the spillover of natural enemies from hedgerows (Roschewitz, Hücker, et al. 2005; (Gaba et al. 2010); Nicholls and Altieri 2013). Increased weed cover could increase the similarity between hedgerow and field communities, with the plant cover providing more shelter for woodland species (Forman and Baudry 1984). The combination of trees and annual crops may also enhance the abundance of natural enemies in annual crops by decreasing the contrast in vegetation structure between hedgerows and fields (Pumariño et al. 2015). Smaller fields and complex hedgerow networks may gain more from the spillover of beneficial organisms, especially if there are ways to make hedgerows more profitable for pollinators and natural enemies than for pests (Bhar and Fahrig 1998; Le Gal et al. 2020). However, beyond the synergies highlighted above, pest regulation may be less effective in more diverse agroecosystems: some authors have shown that predator diversity sometimes leads to intraguild predation, which can result in less effective pest control (Finke and Denno 2004). Thus, more studies on pesticide-free cropping systems and diversified agricultural landscapes will be useful to better identify the impact and location of hedgerows in these more complex environments.

5.5. Hedgerows act as biotic barriers at the landscape scale

Although we have seen in section 2.6 that hedgerows can act as corridors or stepping stones by contributing to the dispersal of certain organisms, they can also represent barriers for the dispersal of others. In this case, hedgerows will be detrimental for certain components of spontaneous biodiversity such as some butterfly species (Fry 1994). Regarding associated biodiversity, hedgerows can hamper the dispersal of pests and of beneficial organisms alike. Reduced movements of carabid beetles (Duelli et al. 1990; Mauremooto et al. 1995; García et al. 2000; Maudsley et al. 2002) and syrphid flies (Wratten et al. 2003) have been documented, and also aphids (Marrou et al. 1979), wind-dispersed pathogenic fungi (Norton 1988; Mossu 1990; Yamoah and Burleigh 1990; Badly and Strigler 1993; Schroth et al. 1995), and bacteria (Schroth et al. 2000).

Whether hedgerows act as corridors or barriers to this dispersal strongly depends on the dispersal characteristics and abilities of the organisms under consideration. Carabid beetles, which are stopped by hedgerows, are mostly ground-dwelling species sensitive to changes in the vegetation structure ("hard-edge" species from Duelli et al. 1990), while syrphid flies usually fly low over the vegetation (Wratten et al. 2003).

The relation between hedgerows, airborne pests (aphids, thrips), and diseases is less clear. These organisms are passively transported by the air currents. Aylor (1990) showed that in the case of pathogenic fungi such as rust, sudden gusts and turbulent air currents were usually necessary to pull the spores off and carry them away. Hedgerow networks reduce the speed of wind (and thus the intensity of gusty winds), while they increase air turbulence between hedgerows (Forman and Baudry 1984). Although hedgerows intercept wind-blown particles, the drop in wind speed on both sides favours air sinking and possibly particle deposition around the hedgerow, especially on the leeward side where the microclimate is more humid and potentially more favourable to pathogens. The same holds true for insects, which, once intercepted by hedgerows, can disperse from hedgerows into adjacent fields, especially near the hedgerow where the wind speed is substantially reduced. Most of the successful examples in the literature (Mossu 1990; Yamoah and Burleigh 1990; Badly and Strigler 1993; Schroth et al. 1995; Schroth et al. 2000) relate to tropical agroforestry systems (alley cropping) where hedgerows are closely spaced (usually 5 metres apart). But more studies are needed to better understand the putative effect of hedgerows as barriers against air-blown pests and diseases for temperate annual crops, for which the effect of hedgerows on wind-blown pests remains unclear.

The negative effect of hedgerows on the dispersal of some beneficial arthropods also remains unclear. Although carabid beetles such as *Nebria brevicollis* (Fabricius, 1792) do not appear to cross hedgerows, they need them for both oversummering and overwintering, and thereafter spill over from hedgerows to adjacent fields (García et al. 2000). Regarding syrphid flies, Wratten et al. (2003) suggested that hedgerows provide them with areas of calm air that represent a favourable foraging habitat. Moreover, it appears that the barrier effect exerted by hedgerows on these organisms depends on their sex and physiology: the dispersal of gravid females and starved individuals is much less hampered by hedgerows (Mauremooto et al. 1995; Wratten et al. 2003).

It appears that hedgerows could act as corridors for some spontaneous species and as barriers for others, including emblematic species such as butterflies. The same holds true for associated biodiversity, although these relations require further study. There might be a trade-off between trapping pests in small fields surrounded by hedgerows but at the risk of preventing natural enemies from reaching it and allowing both pests and natural enemies to spread throughout the landscape. Recognising this trade-off, Bhar and Fahrig (1998) suggested that small fields surrounded by hedgerows combined with pest-suppressive crop rotations may constitute effective pest-regulation strategies. Here again, the relative importance of the different processes will depend on many factors such as soil, climatic conditions, crops or the structure of the landscape.

5.6. Conclusion on the importance of hedgerows in providing regulation services

Although phytophagous arthropods are abundant in hedgerows, few of them are currently of concern to adjacent crops, with the exception of some orchard pests and the agents of crop diseases that have alternative hosts in hedgerows. On the contrary, natural enemies appear quite abundant in hedgerows where they find prey, alternative food resources (nectar and pollen), shelter, and overwintering sites. In many cases, their high diversity in hedgerows is due to partial niche segregation, which allows organisms of the same guild to share space and resources with limited intraguild competition. Pollinator diversity is also high in hedgerows, but hedgerows may be less supportive of pollinator populations than other natural and semi-natural habitats such as flower stripes and meadows.

Few studies report actual positive impacts of hedgerows on biocontrol and pollination services. First, if hedgerows increase the diversity of natural enemies and pollinators, they do not necessarily increase their abundance. Second, although hedgerow pollinators and natural enemies readily spill over into crops, their increased diversity in crops remain often limited to the proximity of the hedge. When important spillover occurs, the subsequent increase in biocontrol and pollination appears to be case-specific and localised. Successful examples have however been reported with aphid regulation by hedgerow parasitoid wasps in annual crops and biocontrol in orchards surrounded by hedgerows. In the former case, hedgerows have a positive impact on regulation services, because they provide ecological functions that are necessary for the beneficial organisms but are not found in the surrounding fields. In the latter case, pollination and pest control are provided by mobile beneficial arthropods that belong to both the spontaneous biodiversity in hedgerows and the associated biodiversity of orchards. It therefore appears that the biocontrol and pollination benefits conferred by hedgerows depend on whether the high spontaneous biodiversity in hedgerows is able to boost the associated biodiversity in nearby crops. This raises the issue of the quality and the quantity of hedgerows necessary to enhance biotic regulation services at the landscape scale and that of their spatial distribution in relation to crops. Several modelling studies point to a positive relationship between the proportion of semi-natural habitats such as hedgerows and their proximity to crops and biocontrol (Delattre et al. 2019; Le Gal et al. 2020) These studies also highlight significant interactions between biocontrol and the life history traits of biocontrol agents (especially their dispersal abilities).

6. Conclusion and perspectives

Hedgerows are uniquely diverse among semi-natural habitats, since they correspond to an ecotone between grasslands, shrublands, and woodlands. They can therefore play host to habitat-specialists from all three types of habitats as well as generalist species that can thrive from the diversity of their microhabitats. Wide and ancient hedgerows with diverse vegetation layers are particularly rich and are therefore key elements to promote spontaneous biodiversity. Such hedgerows are of particular importance for the protection of woodland species in agricultural landscapes. Although the general decrease in biodiversity in agricultural landscapes is well documented (Donald et al. 2001; Green et al. 2005; Butler et al. 2007), few studies have attempted to quantify the impact of hedgerow destruction on this decline (but see Staley et al. 2013).

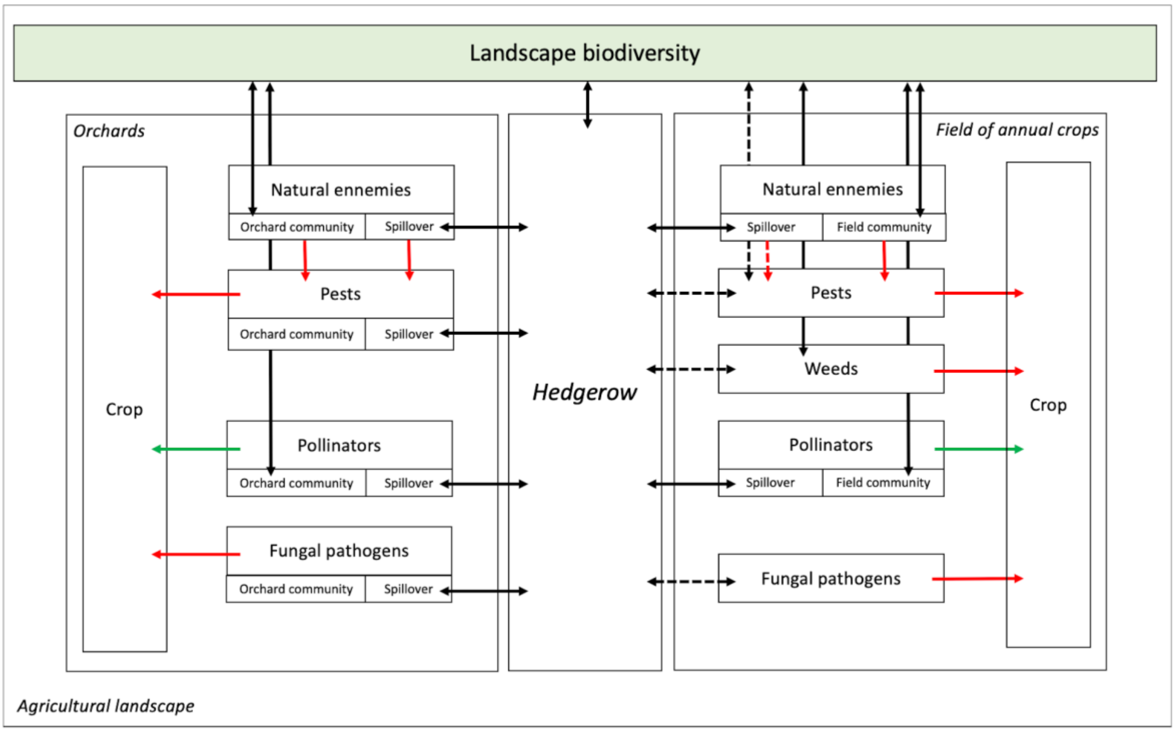

Figure 3: Relations between associated biodiversity and biotic regulation services provided by hedgerows in orchards and annual crop fields identified in our literature review. Black arrows indicate the movement of organisms. Green and red arrows indicate positive and negative relationships, respectively. Solid lines indicate robust relationships, and dotted lines indicate putative relationships. This figure focusses on the effects of hedgerows on the biotic regulation services that they provide in agriculture: interactions between the functional groups of organisms represented here are purposefully not depicted in this figure.

Hedgerows accommodate many taxa, some of which are crop pests, their natural enemies, weeds, and pollinators. The movements of these organisms between hedgerows and adjacent fields appear to be determined by the vegetation characteristics of both habitats such as plant composition, vegetation structure, and presence of trees. Certain life-history traits of the organisms are also determinant for these movements: for example, dispersal ability, need for overwintering sites, or alternative food resources. Crop pests and weeds appear to gain little from hedgerows, and the spillover of pests and weeds from hedgerows into adjacent fields appears to be quite occasional (Figure 3). By contrast, the spillover of natural enemies and pollinators is frequent but only associated with increased biotic regulation services under specific conditions (Albrecht et al. 2020). The shared vegetation structure and mobile arthropod communities between hedgerows and orchards lead to enhanced pollination and pest control services in orchards (Debras et al. 2008; Ricci et al. 2011; Maalouly et al. 2013) and, to a lesser extent, to increased spillover of pests (Figure 3). The strong positive impact of alternative floral resources of hedgerows on fragile metapopulations of short-lived parasitoid wasps also enhances pest control in adjacent crops (Alignier et al. 2014; Morandin et al. 2014).

In many situations, biotic regulation services are performed by different communities in fields and hedgerows, thus limiting their interactions (Figure 3). To understand the relationship between spontaneous and associated biodiversity in hedgerows and neighbouring fields, the specific ecological conditions and trophic networks of each system need to be studied. One robust conclusion, however, is that the plantation of hedgerows is not a solution to the enhancement of all pest regulation services in crops. In some conditions, it could even result in pest enhancement or have other antagonistic impacts. At the scale of the agricultural landscape, hedgerows can contribute to landscape diversification (Figure 3, Bianchi et al. 2006; Dainese et al. 2017), in which the abundance of semi-natural habitats or the level of landscape heterogeneity is usually associated with the increased abundance of beneficial organisms (Pywell et al. 2006; Griffiths et al. 2008; Rusch et al. 2010; Dainese et al. 2017) and associated regulation services (Letourneau et al. 2011; Meehan et al. 2011; Chaplin-Kramer and Kremen 2012; Rusch et al. 2013; Larsen and Noack 2020). The fact that the same organisms may contribute to different ecological functions at different spatial scales blurs the contours of spontaneous and associated biodiversity. Though very useful, a classification of agroecosystem organisms into planned, associated, and spontaneous biodiversity could benefit from considering multiple ecological functions as well as multiple temporal and spatial scales. This raises the question of such a classification, and points to the utility for an integrated, functional, trait-related, spatially-structured, and systemic vision of agroecosystems.

We found that the majority of studies on hedgerows in agricultural contexts have been conducted in temperate regions of Western Europe and North America. Figure 3 should therefore be considered in that context (intensive agriculture, simplified landscapes, broad use of pesticides). It is therefore important to question the results presented in this paper in the context of more diversified agroecological landscapes with less to no pesticide use. It is however interesting to note that studies from tropical agroforestry focussing on alley cropping (at a distance of 5 metres between hedgerows of usually legume trees) yield similar results (reviewed by Schroth et al. 2000), suggesting that the ecological mechanisms identified in Figure 3 may occur in both temperate and tropical regions. A major difference, however, is that pest spillover from hedgerows is more frequent in alley cropping systems (Lal 1989; Grout and Richards 1990; Fernandes et al. 1993; Schroth et al. 1995), which may be related to the proximity between hedgerows and crops (small plots). This may also correspond to a general trend in agroforestry systems (Pumariño et al. 2015).

Other types of semi-natural habitats than hedgerows (such as grass field margins or flower strips) seem to have a more widespread or more regular effects on biotic regulation services. This difference may be due to the fact that hedgerows are rarely designed to provide such services (Albrecht et al. 2020); they rather correspond to pre-existing features in the landscape or are planted for other purposes (Dover 2019). Hedgerows have been shown to provide many other important ecosystem services (Dover 2019), not least of them, recreational, cultural, and educational resources. Some authors argue that hedgerows designed specifically to increase the abundance of beneficial organisms would be more successful for agricultural regulation services (Bugg et al. 1998; Simon et al. 2009; Holland et al. 2016; Holland et al. 2017). However, such managed hedgerows, that will likely be less structurally complex and less diverse than old natural and unmanaged hedgerows, may not be as effective for biodiversity conservation. Therefore, some compromise might be necessary between preserving ancient unmanaged hedgerows that are more favourable to spontaneous biodiversity on the one hand

and planting new planned and managed hedgerows that are more favourable to associated biodiversity on the other. Combining both types of hedgerows in the same landscape would probably help boosting both aspects of biodiversity. Another approach could be to combine unmanaged hedgerows and other semi-natural habitats. Although hedgerows might be beneficial for different communities (Aviron et al. 2018), it has also been demonstrated that their positive effects depend on the landscape context (Bianchi et al. 2006; Garratt et al. 2017). Synergies could be established between hedgerows and other agroecological infrastructures (Griffiths et al. 2008). For example, Hinsley and Bellamy (2000) found that hedgerows are more beneficial for birds when combined with landscape features such as headlands, verges, wildflower strips, well-vegetated banks, and ditches. Similarly, Paredes et al. (2013) observed synergistic effects between crop ground cover and adjacent vegetation on natural enemy abundance. However, the existence of such synergistic effects seems to be case-specific, since several authors failed to detect them between hedgerows and other types of field margins (Merckx et al. 2012; Dainese et al. 2015), or between hedgerows and organic farming (Batáry et al. 2010). More studies are therefore needed to identify the determinants of the hedgerow provision of biotic regulation services and their interactions with other semi-natural habitats and agroecological infrastructures. Their impact in relation to adjacent farming systems should probably also be considered.

Our paper highlights the value of moving beyond the separation between the preservation of spontaneous biodiversity and the promotion of associated biodiversity for agricultural purposes. This separation is useful as a framework for disentangling ecological processes according to functional objectives. But the boundaries between the two types of biodiversity are in fact blurred and may vary depending on the conditions, systems, or scales being considered. Moreover, going beyond this framework could be useful from a philosophical point of view in order to rethink more constructive relationships between agriculture and biodiversity.

7. Author contributions

C.R. and P-A.P. designed the research. P-A.P. performed the research. C.R. and P-A.P. wrote the paper.

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9. Disclosure statement

No potential competing interest was reported by the authors.

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