Dispersal limitation vs recruitment limitation in local assembly rules of plant communities within agricultural landscapes

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Importance relative des processus de dispersion et de recrutement dans la dynamique d'assemblage des communautés végétales en paysage agricole

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Defended on 06 September 2019, after the review of the reviewers and in front of the examination Board:

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إلى أمي وأبي.....

إلى أخوتي حسين ولاء فاطمة محمد.....

إلى قطعتي قلبي عباس وعلي.....

“Rise and rise again and again
like the Phoenix from the ashes;
until the lambs have become lions.”

— Maitreya

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Table of Content

LIST OF FIGURES

LIST OF TABLES

Summary:

The rules by which plant species are assembled into communities is a major issue in ecology. Two different theories explain the presence of a plant species in a given community: the "niche theory" and the "neutral theory". The niche theory is based on the differences between species in terms of their ability to consume available resources where communities are built by the local coexistence of species. On the contrary, the neutral theory considers all species as similar in their community and that "stochasticity" is the main cause of local species composition. More recently, scientists have proposed intermediate models, unifying the two theories and combining stochastic processes and deterministic processes. For a plant to establish itself in a given site, it must succeed in reaching that site and overcome a series of limitations or filtering events. Some species are not present in the focal site because their propagules could not reach the site (dispersal limitation), while others may not be established under the effect of local conditions (recruitment limitation) or not to establish itself durably (persistence limitation). Recruitment limitation may be due to unfavorable abiotic conditions (e.g. harsh environmental conditions leading to environmental filtering) and / or biotic factors (i.e. interspecific interactions of species such as competition, predation or the absence of mutualists). Thus, the assembly of the plant community is the result of regional and local processes. Regional processes are those that determine the group of potential species to colonize (for example, landscape structure, history and heterogeneity). Local processes control the establishment of plant species in actual communities (e.g. biotic and abiotic conditions). The relative importance of the two community assembly processes is debated, with some ecologists believing that recruitment follows the neutralist theory and that the only constraint is dispersal limitation. However, other ecologists consider that recruitment limitations, biotic interactions and abiotic conditions are more important than dispersal.

Today, fragmentation and habitat loss are considered a major threat to biodiversity in global terrestrial ecosystems. Fragmented habitats are characterized by reduced population size and extinction events. With the increase in human activities, species extinction rates are higher than in previous records. Fragmentation is defined as a complex process by which a large continuous habitat is divided into many smaller and smaller plots. Fragmented habitats are separated by a matrix that differs in structure and composition from the large original habitat. Most researchers described the negative, qualitative and quantitative effects of fragmentation on different habitat types (e.g. forests). However, other studies have indicated that habitat fragmentation may have a positive effect on increasing species richness locally and regionally, due to crowding effect. In the context of reducing the effects of habitat fragmentation, several questions may arise and require attention before taking action. Is it better for fragmented habitats to be connected to dispersal corridors or left as self-evolving isolates? Is it better to preserve a single large area or several small isolated biological reserves (SLOSS)?

Forest fragmentation occurs when a large continuous forest is split into two or more small forest patches surrounded by a non-forest matrix. At the global level, it is thought that forest fragmentation affects the sustainability of ecosystems (e.g. global species diversity). As long as fragmentation continues, several local processes are affected (local species richness, interspecific interactions, seed dispersal, and local microclimate).

Large populations of understory vascular plant species characterize forests and these include forest specialists, who play an important role in the functioning of ecosystems (e.g. nutrient cycling and organic material). However, the current fragmentation of forests threatens this relationship between biodiversity and ecosystem functioning throughout the loss of habitat. As a result, the impact of forest fragmentation on local (i.e. alpha) and larger (i.e. gamma) diversity has been widely studied in forest ecosystems. However, the impact of forest fragmentation on the alpha-gamma relationship remains totally unknown. The study of this alpha-gamma

relationship, rather than alpha and gamma diversity separately, makes it possible to evaluate the relative importance of local processes and, on a larger scale, for the assembly of the community. Surprisingly, no one has ever verified whether forest fragmentation shapes the alpha-gamma relationship and in which direction. Answers to this question could help provide clear management guidance to limit the adverse effects of forest fragmentation on biodiversity and thus the functioning of ecosystems. By comparing the impact of forest fragmentation on the alpha-gamma relationship of vascular plants for specialist and general forest species, we bring here, for the first time, clear answers to this topical issue.

To help answer our study question, we compared the alpha-gamma relationship of both forest specialists and generalists between different regions in North France (Hauts-de-France) differing in spatial resolution (species pool) and landscape context, i.e. non- (fake patches within a forest matrix), semi- (small, connected patches within a matrix of grasslands) and highly-fragmented (small, isolated patches within a matrix of crop fields) systems. Noteworthy, we used the most recent scientific advances to analyse the alpha-gamma relationship (i.e. the log-ratio model developed by Szava-Kovats, R. C., Ronk, A., & Pärtel, M. (2013). Pattern without bias: local-regional richness relationship revisited. Ecology, 94(9), 1986–1992. doi:10.1890/13-0244.1).

We found a clear interaction between the level of fragmentation of the forest and the type of species (specialist or generalist) on the form of the alpha-gamma relationship, the fragmentation of the forest being detrimental to specialist species and benefiting generalist species. . Indeed, the alpha-gamma relationship of forestry specialists has shifted from a linear form (proportional sampling) to a low degree of fragmentation, to a curvilinear form (community saturation) with a high degree of fragmentation. This suggests that diversity in forest specialists, within their most preserved and functional habitats (non-fragmented systems or strongly connected forest plots), is more influenced by large-scale processes related to dispersal, biogeography and

species evolution rather than local and more deterministic processes such as competition and environmental conditions.

Based on our findings, we affirm that the conservation of a network of highly interconnected forest patches, particularly fragments of old-growth forest, should be a priority target for the long-term conservation of forest-dwelling species, which are also the most endangered species in the context of forest fragmentation and intensification of agricultural landscape management. Our findings have strong implications for biodiversity conservation and landscape management, suggesting that the strategy of maintaining or restoring connectivity between forest plots through a dense network of hedgerows would benefit mainly to forest specialists.

The challenge of the 21st century, and especially since the green revolution, is to meet the growing demands for food while reducing the negative impacts on the environment. Intensive farming practices using excess pesticides and fertilizers, associated with severe soil disturbance, have had adverse effects on biodiversity in plant communities. Therefore, there is an urgent need to find alternative farming techniques that respect the environment, while maintaining or even increasing crop yields. Integrated weed management systems are thought to be promising in that they aim to provide high yields and less environmentally damaging crops by using biological, less chemical and less mechanical approaches. The use of different cover crops (CC) with reduced tillage practices offers a range of environmental benefits such as soil erosion prevention, weed control, increased fertility soil, improving the nitrogen cycle, increasing the soil organic matter content and maintaining high yields. However, our knowledge of how different CCs (such as *Camelina*) and reduced tillage practices affect the assembly of weed communities in agricultural landscapes is still limited. Thus, experimental approaches studying the effect of different CCs and different tillage practices on the occurrence and persistence of weeds help to better understand the response of weed communities to different farming practices.

In this chapter, we present a controlled experiment (specific composition and propagule pressure) aimed at evaluating the combined effect of different tillage techniques (simplified soil work reduced vs. no tillage) and rotations of the cover soil (two CC vs no CC) on weed community assemblage and crop yield in sunflower crops. To this end, we have set up a controlled experiment using a random block plan, with rotation between barley, sunflower and wheat crops, either with *Camelina sativa* in intercrop or with winter plant cover. Mixed leguminous, inserted between barley and sunflower. We assume that winter CCs along with less tillage could have significant weed control activity (via allelopathy and / or diversity complementarity), while improving sunflower yields.

We followed diachronically the richness and abundance of weed species, the change in their relative abundance compared to an initial state (change of abundance rank) and, at the end of monitoring, measured the sunflower yields (height of sunflower and weight of sunflower seeds per stem). Using generalized linear models, we analyzed the effect of soil cover and tillage on weed species richness, abundance, and sunflower yields. For relative abundance change, we used mixed-effect linear models to compare the relative abundance change with the baseline. Our results support some of the proposed hypotheses that winter CC-mix removes the most dominant weed species by the diversity complementarity rather than an allelopathic effect of camelina. A CW in winter does not affect species richness, while soil preparation appears to impact species richness of weeds in a complex way. In addition, the use of *Camelina* as an intercrop enhances the relative abundance of patrimonial species at the expense of noxious species. Finally, the winter CC has a positive effect on the yield of sunflower crops while *Camelina* shows a contrasting effect.

A decline was recorded in the biodiversity of natural ecosystems because of human-driven extensive alterations and conversions (e.g. intensive and expansive agricultural practices leading to environmental degradation). Over the past 40 years, conservation ecologists have

increased the awareness about the importance of maintaining the biodiversity and ecological processes delivered by natural ecosystems. Ecologists have focused on the maintenance of native ecosystems as a conservation strategy facing landscape transformation. Habitat corridors (e.g. hedgerows) as a landscape feature promoting connectivity between isolated habitat fragments are considered one of the strategies for conserving biodiversity in fragmented landscapes.

Most forest herbs are perennials with long-living lifecycles. However, they are showing an increase in their vulnerability for extinction events due to increased forest fragmentation. Forest herbs are stress-tolerant and characterized by higher tolerance to low light availability. In addition, forest herbs are characterized by lower germination rates, lower seed production and lower long-ranged dispersal events. All these limitations interfere in the assembly and long-term persistence of forest plant species.

In agricultural landscapes, it is suggested to maintain hedgerows as corridors that would allow the movement across the forest patches. Hedgerows are considered forest-like habitats that may represent a potential refuge for forest specialist species. However, the knowledge about the extent to which hedgerows are suitable habitats for the germination and persistence of forest plant species is still poor and debatable. The idea of hedgerow possibilities for acting as a corridor for forest specialists falls between three theories. The first theory assumes that almost all hedgerows are suitable habitats that ensure the conservation of forest species. The second theory states that hedgerows are subjected to intensive human disturbances making them highly different from forests in the context of forest species conservation. The third theory is an intermediate theory assuming that hedgerows may provide a suitable habitat for a subset of forest plant species. The intermediate theory was suggested due to the low dispersal capacity of forest plant species requiring large time intervals to reach the hedgerow. Trying to solve this debate, we had made this study aiming to increase our knowledge about the possibility of forest

specialists to be presented in hedgerows. Assuming that forest specialists are dispersal limited, we implemented this controlled experiment where several forest plant species were sown in both recent hedgerows and open field landscapes to study the dispersal and recruitment limitations. In the same hedgerows, we performed transplantation experiment to test the persistence limitation of forest plant species by comparing their persistence between both hedgerows and forest. For the two tested approaches (i.e. germination and persistence), we had studied the possibility of biotic interactions (i.e. competition) by removing resident vegetation from one side of the transect (5 transects of hedgerows and 2 transects of forest) and keeping them on the other facing part of the same studied transect.

Our study is still underway and needs longer-term follow-up to properly assess the possibility for hedgerows to serve as corridors for forest species. Our preliminary results show that few planted species have established themselves in hedgerows, suggesting that the presence of a species in hedgerows is subject to both dispersal limits and recruitment limits.

Chapter 1: General introduction

1.1. Background

One challenge for ecologists is to understand the abundance of species, their distribution, and their interaction with other species. Community ecologists concentrate on the scale at which species locally assemble. Habitat fragmentation as a world widespread phenomenon has fostered the study of metacommunity dynamics. A metacommunity is defined as the set of interacting (or interconnected) local communities that are linked (or connected) by species dispersal and into which species have the potential to interact with each other (M. A. Leibold et al., 2004b). The theory of metacommunity tries to explain the scale-dependent processes patterning species assemblages. The change in spatial dynamics of local communities may directly and indirectly alter local community processes (Jackson & Blois, 2015). This is why it has been a challenging question in metacommunity ecology to study how local processes affect patterns observed at landscape to regional scales. The concept of metacommunity relies not only on how species interact within local communities, but on how spatial heterogeneity and disturbances lead to the formation of suitable habitat patches within a matrix of non-suitable habitats (Van Teeffelen, Vos, & Opdam, 2012). Metacommunity ecologists seek to understand the types of interactions at different spatial scales, the relative importance of these species-specific interactions and the effect of species' dispersal abilities in patterning natural communities (**Chapter 2**) (Rajala, Olhede, & Murrell, 2018).

Plant communities are major key players in all ecosystems on Earth, and are considered at the basis of global food and biogeochemical cycles. Therefore, within plant communities, plant species may affect each other's behavior and consequently affect the overall functioning of the community and abovementioned biogeochemical cycles (Fig. 1D & 1E).

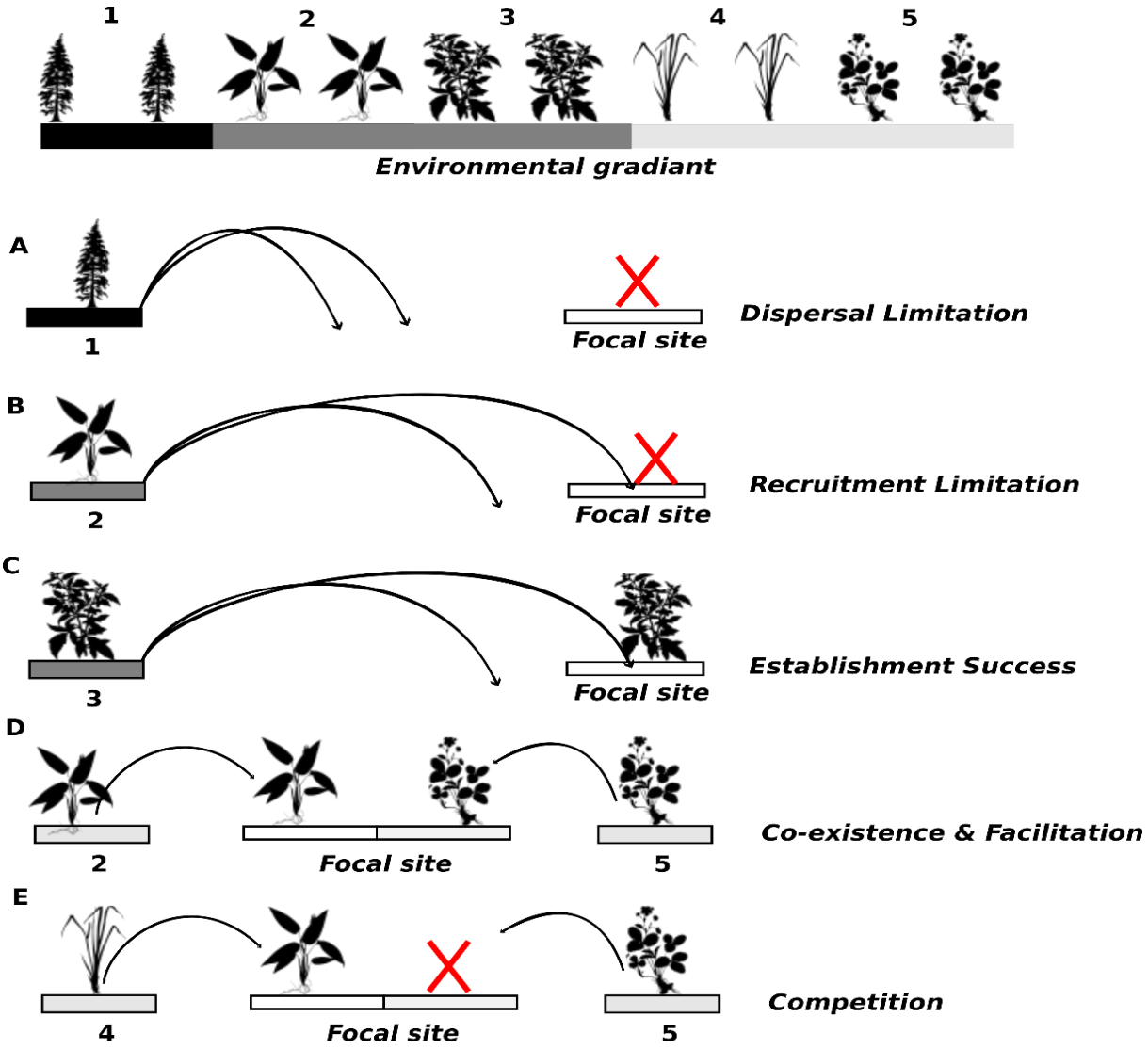

Figure 1-1: Community assembly processes affecting species' occurrence and abundance across an environmental gradient. (A)*: The species is absent from the focal site because of dispersal limitations.* ***(B)****: The species is absent from the focal site due to recruitment limitations because it can disperse there.* ***(C)****: Establishment success is achieved once dispersal and recruitment limitations are overcome.* ***(D)****: Plant-plant positive interactions (e.g. facilitation) may foster species co-existence once dispersal limitations are overcome. E: Plant-plant negative interactions (e.g. competition) may limit species co-existence even after dispersal limitations are overcome. Figure inspired from Zobel (1997) and Lortie et al (2004).*

In addition, the occurrence of a given plant species within a given plant community depends on the abiotic conditions of the habitat hosting this community, which should meet all

conditions (e.g. microclimate & soil properties) required by the plant to germinate and persist locally (i.e. successful establishment) (Fig 1-1B) with anthropogenic or natural disturbances potentially disrupting the local abiotic conditions. Therefore, we need to understand the processes that shape and influence these plant communities in order to manage them in a sustainable manner.

Several attempts have been made to generate general rules explaining species distribution across a given landscape. MacArthur and Wilson´s theory of island biogeography was one of the first attempts in fixing ecological assembly rules that control local species assemblages (Wilson & MacArthur, 1967). Ecological assembly rules consider that plant assembly results from the effect of three biological filters acting on a regional species pool: dispersal (Fig. 1-1A); abiotic environmental conditions; and biotic interactions (Fig. 1-1B & 1-1C) (Götzenberger et al., 2012; Weiher & Keddy, 2004).

Several questions arise starting from the fact that plant species are living in a complex web of interactions inside ecological communities. What is the effect of the environment itself on the germination success and the relative abundance of a given plant species within a given community? What are the effects of a given species on the other species of the community and how strong is its impact? How can it be possible for different species to coexist in the same community? What pattern of species composition and level of species diversity can we observe if community structure is strongly affected by species interactions? These are common questions tackled by ecologists. Thus, increasing our knowledge about the processes that control the assembly of plant communities supposes that we assess the effect of each filter alone and its interaction with other filters (e.g. plant-environment interactions, plant-plant interactions) at different spatial scales.

Community structure can be described via species richness (i.e. species diversity or species density) (Kelt & Vuren, 1999). Another measure reflecting ecosystem properties is

aboveground biomass (i.e. a proxy for productivity). Combining these two measures (Fig. 1-2) into an ecological study is a common approach (Newbold et al., 2015); this will be discussed extensively in **Chapter 3**.

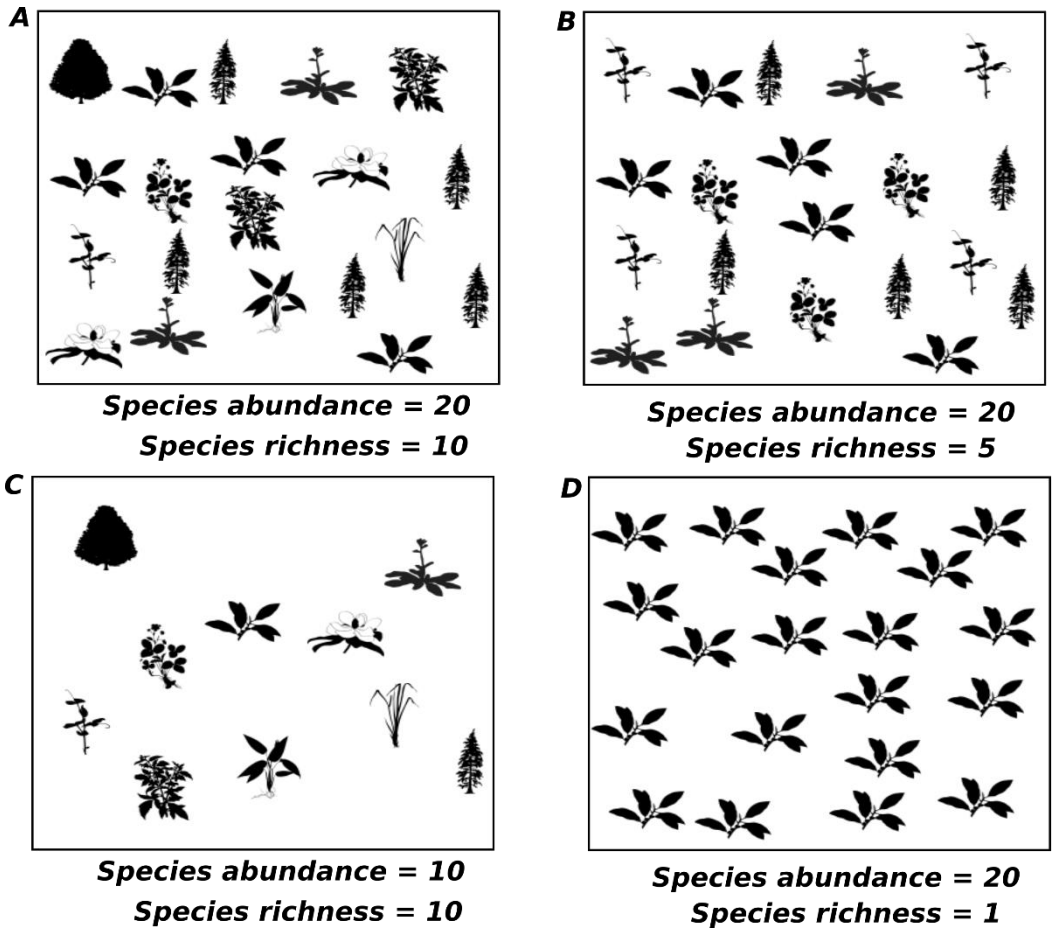

Figure 1-2: Species richness and species abundance are two metrics used for evaluating communities. (A)*: Fictive plant community with the highest species diversity and species abundance.* ***(B)****: Another fictive plant community showing lower diversity while abundance is the same as* ***A****.* ***(C)****: A plant community represented by high diversity (same as in* ***A****) but with lower species abundance than in* ***A*** *and* ***B****.* ***(D)****: A plant community represented by one siingle species (monoculture) although it is a highly abundant species. Community* ***A*** *is considered more diverse than other communities in the sense of community structure and ecological properties. Community* ***D*** *is characterized by the dominance of one species (monoculture) and a very low resilience of ecological properties. Communities* ***B*** *and* ***C*** *fall in the continuum between communities* ***A*** *and* ***D*** *in terms of community structure and ecological properties.*

Several theories exist on the relationship between species richness and species productivity, such as: the "dynamic equilibrium" model (Huston, 1979); the "humped back" model (J. Philip Grime, 2006a; Hodáňová, 1981); and the "resource-ratio" or "R*" model (David Tilman, 1982). Despite differences, these models all assume a unimodal relationship between plant species richness and aboveground biomass (Adler, Seabloom, Borer, Hillebrand, Hautier, Hector, Harpole, Yang, et al., 2011). Several recent studies examined the relationship between plant species richness and aboveground biomass (S. Li et al., 2018; Yu Li et al., 2019; Venail et al., 2015). Hooper et al. (2012) showed that a 21-40% decrease in local plant species richness might lead to 5-10% reduction in biomass production. However, reducing the local biodiversity by 60% induces a greater decline in biomass production. Similarly, Liang et al., (2016) discussed the biodiversity-productivity relationship (BPR) in forest ecosystems, and showed that a 10% reduction in tree species richness led to a loss of 2-3% in the aboveground biomass of trees, while decreasing species richness down to a single species (monoculture forest) led to a decrease of 26-66%. In addition, Newbold et al., (2015) stated that local species richness is more likely to be affected and consequently affecting biodiversity, where the average local species richness declined by 13.6% because of land use and anthropogenic activities. In addition, some areas were more affected showing a decline of 31%, which is enough to affect ecosystem functions and services.

1.2. The niche-neutral debate

Within a given habitat patch, two or more species may be absent and thus cannot co-exist locally as parts of a given community of the focal habitat patch. This can happen because one species outcompetes the others and excludes them from the local community; or simply because the habitat patch does not match the species' autecological requirements. Two opposite theories have influenced assembly rules: the *niche theory* and the *neutral theory*. Different definitions

for the ecological niche have been advocated by different ecologists (Elton, 1927; Grinnell & Swarth, 1913; G. E. Hutchinson, 1961). Each definition is unique in some way, but all state that not all species interact similarly with the environment, and that the species-environmental interactions are the main attributes to assess when studying ecosystem structure.

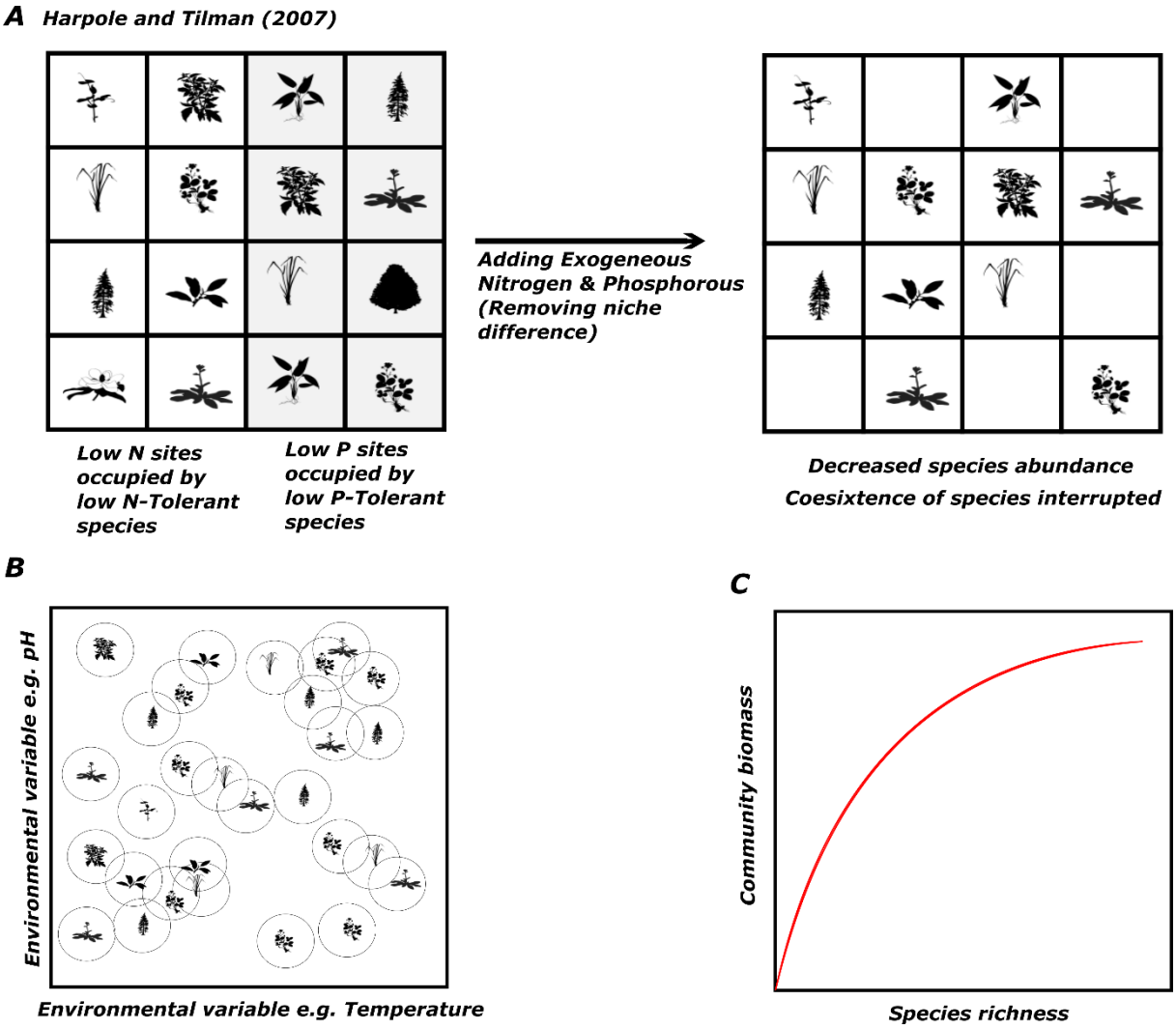

Figure 1-3: Three different illustrations revealing the importance of niche difference in affecting species abundance and coexistence. ***(A)****: Illustration of Harpole and Tilman (2007) experiment.* ***(B)*** *: This represents the "snowballs in the barn" model of niche differentiation and coexistence. The circles in* ***(B)*** *represent the range of conditions of every species.* ***(C)****: This represents an analytical curve explaining the relationship between species richness and community biomass. Inspired from Tilman (2000).*

According to the niche theory, species co-existence is stabilized by density-dependent interactions and the species composition may remain steady for a long time in the absence of external disturbance (Chesson, 2000a). Niche complementarity is one of the mechanisms suggested to explain the relationship between plant species diversity and ecosystem functioning (Huston, 1979; Loreau et al., 2001a). This mechanism suggests that species exploiting various resources (e.g. species with different strategies in nutrient use or species differing in phenology or physiology) will be able to coexist, thereby increasing species richness and resource uptake, and thus productivity (Bruno, Stachowicz, & Bertness, 2003; Kareiva & Bertness, 1997). Tilman, (2000) explained niche differentiation and species coexistence using the "snowball on the barn" model (Fig. 1-3B and 1-3C). Niche differentiation causes an increase in plant diversity, which will in turn predict an increase in the plant community productivity. Every species exists in a defined range of conditions (circles of the model), and two or more species can share a subset of these conditions (intersecting circles) forming heterogeneous communities. The more heterogeneous the community is; the more diverse plant community will be. In addition, increased diversity will cause an increase in the coverage of habitat conditions, resource uptake efficiency and eventually total plant community biomass (Fig. 1-3C). Another study of grassland communities by Harpole & Tilman (2007) explains the impact of the differences among species niche requirements (nitrogen and phosphorous) on their abundance and distribution (Fig 1-3A). In this experiment, species are categorized according to their tolerance towards low nitrogen and phosphorous availability. In case of nitrogen (or phosphorous) depletion, one of the species will be a superior competitor over the other, facilitating their coexistence. However, in the same experiment, plant species abundance decreased when nutrients were added so that neither phosphorous nor nitrogen were limiting anymore. Species were no longer able to balance between the available space and their niche requirements, making it harder for them to coexist. Therefore, understanding the patterns of

plant species abundance and distribution requires accurate information about species dispersal, niche requirements, stress tolerance and reproduction (Di Musciano et al., 2018).

The neutral theory in explaining species abundance is as old as the niche theory, but the attention for the neutral theory was raised after Hubbell (2001)'s book "*The unified natural theory of biodiversity and biogeography*". Several studies adopted this theory to explain patterns of local species diversity in a metacommunity context (Leigh, 2007; Rosindell, Hubbell, & Etienne, 2011). The neutral theory assumes that all species are identical in terms of niche (McGill, 2003; Volkov, Banavar, Hubbell, & Maritan, 2003), and that species abundance and distribution are only under the dependence of stochastic processes (Fig 1-4), namely immigration, death, birth and speciation rates (Hubbell, 1997). Moreover, the neutral theory is based on two assumptions: saturation and neutrality (Etienne, 2007). Saturation means that the community size is fixed with time scale and the number of species inside is finite (Cornell & Lawton, 1992). In addition, saturation states that resources are fixed and none of these resources is left without being consumed as long as communities are undisturbed (Hubbell, 2001). Secondly, neutrality states that species inside the community are functionally equivalent. Therefore, neutral theory assumes that species compete equally and randomly for space (speciation and immigration) (Chave, 2004).

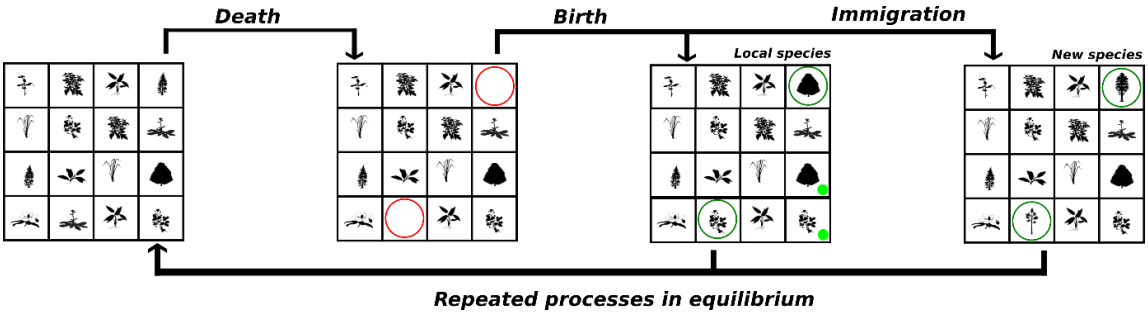

Figure 1-4: Death, birth and immigration cycle in the neutral theory. *Red circles represent the dead species locations. Green circles represent the new species occupying the space left by the dead species. Green dots represent the origin from which new species came. Figure modified from Rosindell, Hubbell, and Etienne (2011).*

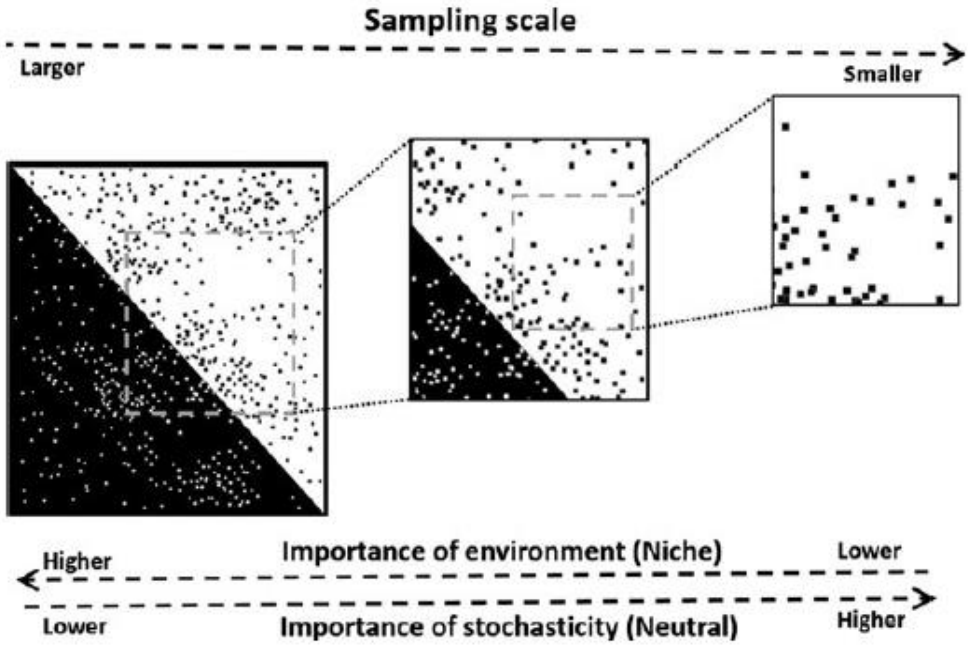

Figure 1-5: Schematic diagram describing a prediction about the effect of sampling scale on the relative importance of environmental (niche) factors and stochastic (neutral) factors. *The community in this diagram is represented by two species (black and white). Black species are favoured by the environmental conditions restricted to the black zone (lower left half). White species are favoured by the environmental conditions restricted to the white zone (upper right half). Habitat association appears to be very strong at largest scale, where several individuals of each species may be found in their less favoured habitats (black and white squares on the sides opposite to their favoured habitat). At intermediate scales (middle panel), habitat association is still having an impact on the studied community. However, at the smallest scales, one habitat type appears to be eliminated (species favoured by black habitat) with few remaining individuals are distributed by the effect of stochastic processes. Figure from Chase (2014).*

Biodiversity loss due to environmental disturbances highlights the importance of studying species abundance and coexistence in both space and time (Cordonnier, Kunstler, Courbaud, & Morin, 2018; Weiher et al., 2011; White, Montgomery, Pakeman, & Lennon, 2018). Between niche-based and neutral-based community assembly rules, a trade-off may better explain the patterns of species distribution by treating both processes as two ends of a continuum (Fargione, Brown, & Tilman, 2003). While niche-based local processes are

fundamental in studying plant community composition, dispersal and neutral processes are essential by being the first events before species can even establish in a community, especially so in disturbed communities with ecological alterations (Brown & Kodric-Brown, 1977a; Thrush, Halliday, Hewitt, & Lohrer, 2008). Increased dispersal makes local communities reachable and allows the immigration in and emigration out of species (Mouquet & Loreau, 2002). Immigration and emigration may affect both local gains and local losses of species (M. A. Leibold et al., 2004b). In addition, immigration will lead to the establishment of new species with different resource demands and uptake strategies, thus fostering niche complementarity (explained above). Other studies (Chase, 2014) had shown that the sampling scale better explains the relative importance of environment (niche) and stochasticity (neutral) (Fig 1-5). Therefore, the applicability of these two theories depends on the size of the species pool, environmental conditions and the spatial scale at which community is assessed. Niche and neutral processes operate simultaneously rather than alternatively.

1.3. Community assembly concepts

Community assembly seeks to understand the processes shaping local communities at the level of species identity and abundance. Community assembly rules start with the species pool concept that had been subjected to several "filtering events" before it becomes the actual studied local community. Several studies tried to understand the effect of dispersal, biotic interactions and abiotic conditions in shaping local communities and filtering the regional species pool (Woods & McGarvey, 2018). Community assembly involves two sets of filters with (1) biogeographic processes encompassing the first set of filters directly shaping the species pool from global to regional scales (e.g. migration, extinction and speciation) and (2) ecological processes encompassing the set of filters by which the actual community is obtained from the regional species pool (Figure 1-6) (Karger et al., 2016).

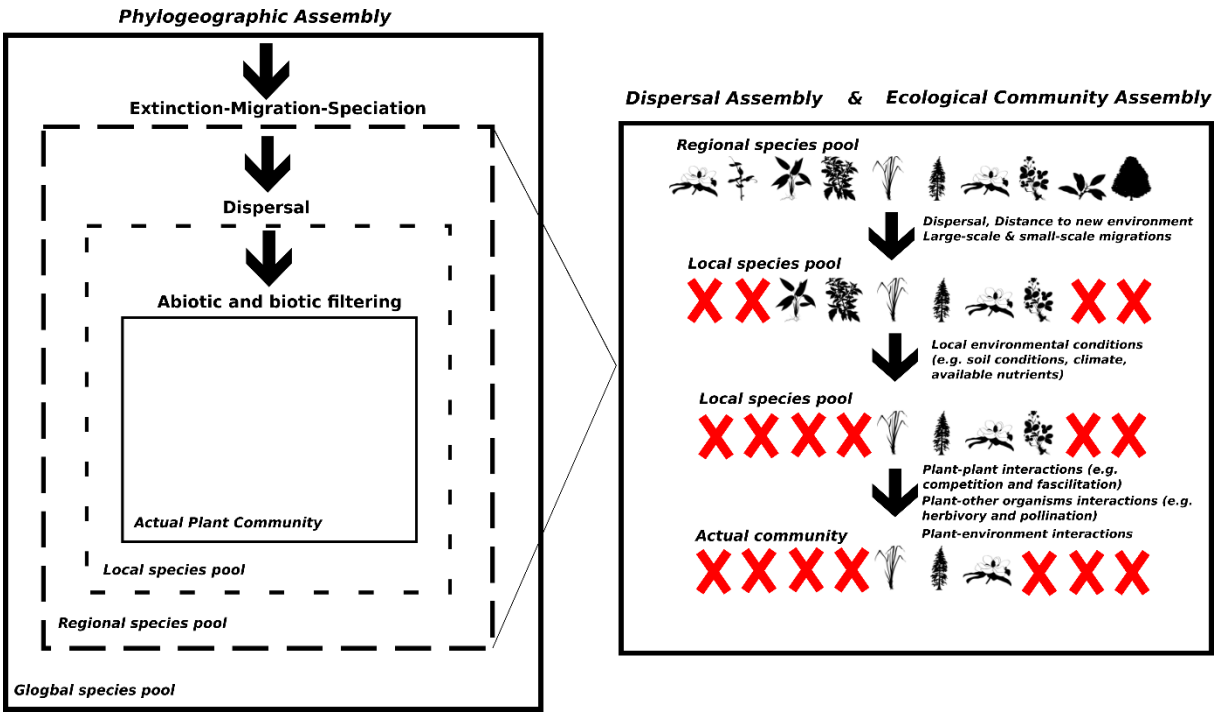

Figure 1-6: Processes behind community assembly rules and their corresponding scales. *The regional species pool is a subset of the global species pool obtained after the first set of filters has been applied (i.e. extinction, speciation and migration) (referred to as phylogeographic assembly). The local species pool is a subset of the regional species pool obtained after accounting for dispersal filters (referred to as dispersal assembly). Actual studied communities are the result of both biotic and abiotic filtering defining the actual assemblage of plant species (referred to as ecological assembly). Adopted and modified from Zobel, (1997).*

In the context of plant ecology, community assembly rules were defined as the non-random patterns of community structure caused by both biotic interactions and environmental conditions (Weiher & Keddy, 2001). In a general sense, assembly rules encompass any filter altering the regional species pool (Diaz, Cabido, & Casanoves, 1999; Keddy, 1992; Weiher & Keddy, 1999, 1995). Keddy, (1992) reviewed community assembly as a process of deletion, where abiotic conditions and biotic interactions are considered nested sieves sorting species from the regional species pool depending on their habitat requirements. Consequently, species having specific functional characteristics and matching a specific set of filters will be able to colonize and assemble into a given plant community. However, Wilson & Gitay (1995) restricted the definition of community assembly rules as "the restrictions on the presence or

abundance of a certain species in a community due to the presence or abundance of other species, or group of species". According to Zobel, (1997), community composition is based on a combination of broad and small-scale processes (Fig. 1-6).

The broad-scale processes (e.g. extinction, speciation and migration) are the key factors determining the size of the regional species pool that is available for communities to assemble (Fig. 1-10 & 1-5). At a smaller spatial scale, the actual species composition is constrained by dispersal, abiotic conditions and biotic interactions, that act as nested sieves, through which the species are sorted. Lortie et al., (2004) proposed the "Integrated community concept" stating that four different processes (biogeographical events, local environmental conditions, plant interactions and direct interactions with other organisms) control the magnitude of variation within a plant community over space and time.

Two concepts of community assembly are thus central in analyzing any plant community. The first one is the "species pool" concept, which is defined as the group of available species that have the potential to colonize in the local site being studied (Connor & Simberloff, 1979; Strong Jr, Szyska, & Simberloff, 1979). The second one is the "filter" or "sieve" concept which is represented by the biotic or abiotic conditions that affect the establishment of plant species in the local site (Woodward & Diament, 1991).

1.3.1. Dispersal

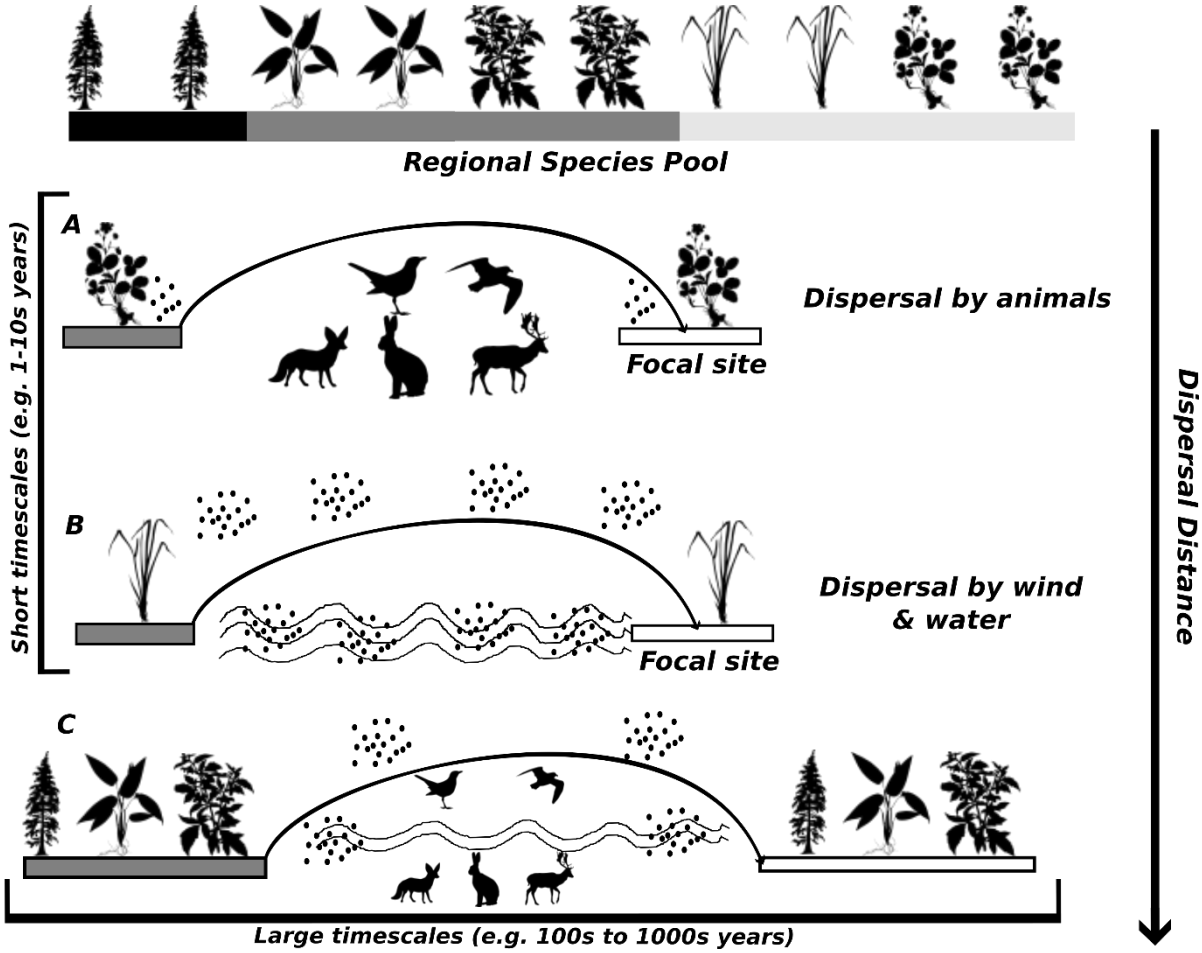

Figure 1-7: Different dispersal mechanisms depending on the time scale considered. (A)*: dispersal by animals over short time periods.* ***(B)****: Dispersal by wind or water over short time perios. It depends on both dispersal distance and dispersal mechanism for dispersal to occur. For short or moderate distance dispersal it may take tens of years.* ***(C)****: For long distance dispersal, it may need hundreds or thousands of years for a species to disperse to another site. Inspired from Hämäläinen et al., (2017).*

Dispersal is defined as the process by which an organism will transport the next generation across space. For sessile organisms like plants, this is the only way to physically move, through immigration of the next generation in the community and through emigration out of the community by means of local extinction (Nathan et al., 2008). Another general definition states that dispersal is the movement of an individual organism from its birthplace to the location where it will germinate, reproduce and have offspring (Pearson & Dawson, 2005). Plant

dispersal occurs only at the seed or propagule stage of the plant life cycle. After germination of the seed for seed-bearing plants, the individual settles down in a specific location where it will spend the rest of its life. As stated above, dispersal is considered a primary component of community assembly. It is thus important when studying dispersal ability of a certain species to take into consideration the different aspects of the dispersal process (i.e. dispersal mechanisms, dispersal distance and impact of dispersal on community assembly).

Seed dispersal implies several mechanisms (Fig 1-7A & 1-7B) including dispersal by animals, wind, gravity (i.e. seeds that fall below the germinating-source plant) and water. Most flowering plants use animals to carry their seeds (i.e. seeds carried on fur or feathers, seeds contained in eaten edible fruits and deposited later through droppings), over short or long distances. It has been shown that interaction with animals, especially the super diverse taxonomic class of insects, have helped flowering plants to become the most successful plants on earth (Tur, Castro-Urgal, & Traveset, 2013). Wind dispersal mechanism is considered important for small, dry and hard plant seeds (e.g. Milkweed). Although wind-dispersed plants produce large number of seeds with high wind-dispersal ability, most seeds will not germinate and the large number is to ensure that at least some will grow and eventually produce seeds themselves. In addition, phenotypic functional traits of seeds may assist wind dispersal; for example, maple winged fruit seeds act as kites and propellers that aid in wind dispersal for long-distance locations. Several other factors control the distance of seed dispersal by wind, such as horizontal wind speed, the height of seed release and seed terminal velocity (Soons, Nathan, & Katul, 2004). By investigating wind dispersal distance in fragmented habitats, Bohrer, Katul, Nathan, Walko, & Avissar (2008) suggested that long-distance dispersal might increase the survival of populations having intermediate probabilities of local extinction. Concerning water dispersal, seeds of some plants (e.g. *Carex* spp, *Epilobium tetragonum*) float and travel on water bodies (with the dispersal distance which varies depending upon water stream features) before

being washed up on the river banks and germinating if conditions are suitable (Araujo Calçada et al., 2013a). In most cases and with the various dispersal mechanisms, seed are undirectedly dispersed with respect to suitable sites for the plant to germinate and subsequently establish (random dispersal) (Howe & Smallwood, 1982).

It is believed that the impact of dispersal on community assembly is time dependent (Fig 1-7C). In other words, the probability of a certain species to disperse to distant sites increases with the temporal extent considered (Jacquemyn, Butaye, & Hermy, 2001), and hence the establishment of plants in new communities at short spatial distances from seed sources can occur within short time scales (few years) while the establishment at long distance through long-distance dispersal (LDD) events is likely to occur over long time scales (from centuries to millennia). Some plant species (i.e. short dispersers) may have capacity for LDD events to happen but it depends upon the combination of dispersal mechanism and time interval (Schurr et al., 2016). In their study Schurr et al. (2016) used two parameters: seed-dispersal retention time (i.e. the amount of time spent by the seed inside the vector before being translocated to the focal site) by the vector (P), and the vector's velocity relative to the dispersal retention time (V). For example, seed dispersal with higher velocity mechanisms (e.g. large and fast vectors like mammals, birds or strong wind activity with elevated seed heights) results in LDD as long as retention time (P) is high. In the community assembly context, several studies assumed that plant species belonging to a given regional species pool have the capacity to disperse at any location over the corresponding region when considering a sufficiently long time (Fenchel & Finlay, 2004; Nekola & White, 1999; J. J. Wiens & Donoghue, 2004). Consequently, community assembly patterns would mostly rely on local biotic and abiotic interactions after dispersal being achieved, making these interactions crucial to determine the local community composition and species abundance.

1.3.2. Abiotic conditions are "filters" for potential recruitment once dispersal happened

Abiotic conditions are considered a major process in "filtering out" species by exerting several limitations on species establishment and survival. Plant species show a wide variety of requirements to germinate and establish in a certain community. These requirements include, among other things, soil nutrients, light conditions, water availability and climate conditions in all its components (e.g. humidity, moisture and temperature).

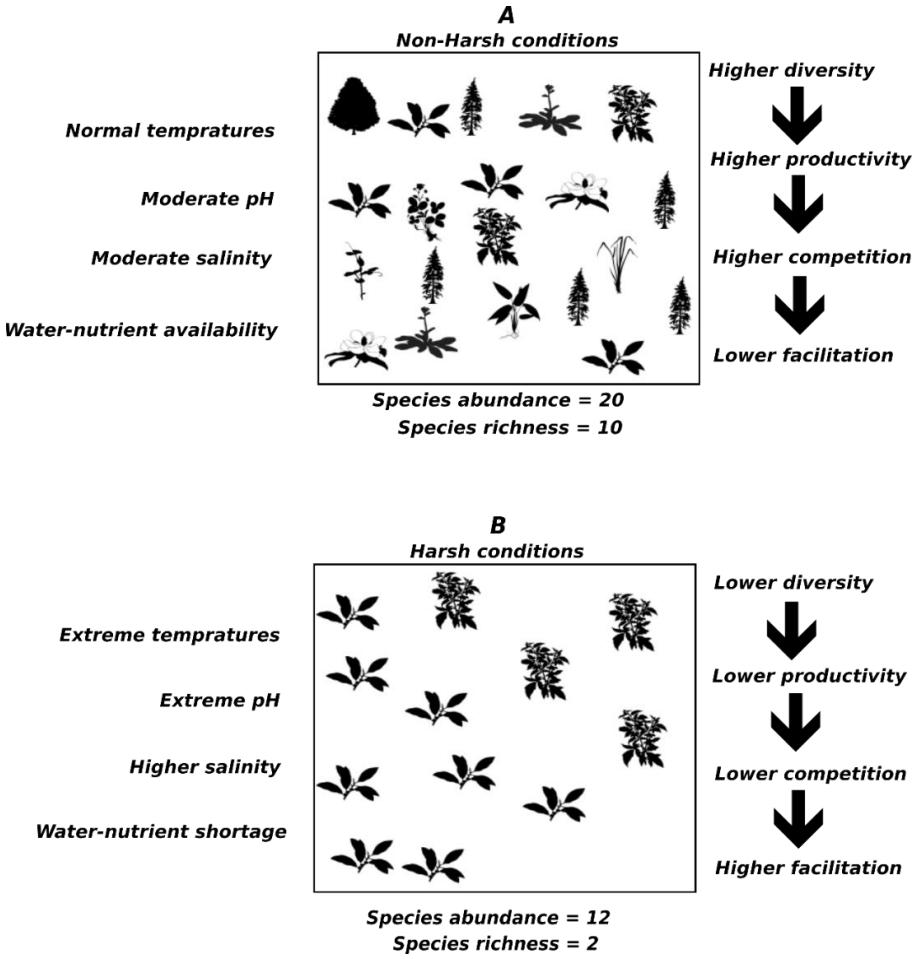

***Figure 1-8: Two different plant communities showing different environmental conditions. (A)**: In communities with non-harsh conditions, species diversity is high leading to higher productivity and competition and eventually lower facilitation. **(B)**: Communities in harsh conditions (**B)** induce lower diversity leading to lower productivity and lower competition, and consequently facilitation will be more important.*

Following dispersal, seeds of plant species might reach a location where condition are unsuitable for their germination and the subsequent survival of the individual, so that the species fails to recruit. It may be the result of one or a combination of abiotic factors that limit the presence of a species in the local community. However, when conditions are unsuitable, some species might have the ability to incorporate the soil seed bank as a dormant diaspore waiting for conditions to become suitable to germinate (Willson & Traveset, 2000). Therefore, assessing the soil seed bank species composition is needed to confirm the presence or absence of a given species at a given site, although there still a wonder in considering seed bank in local measurements (Plue et al., 2017). Some species may establish despite unsuitable local conditions, via a mechanism called "mass effect" (Waller, Mudrak, & Rogers, 2018). In such a case, the locally established population acts as a sink population (Pulliam, 2000). This mechanism appears at different sites connected by dispersal, where species flow from habitats with higher quality to habitats that are less suitable. The mass effect may allow species to locally coexist with species having different ecological requirements (Waller et al., 2018), hence providing support to the neutral theory of Hubbell, (2001) and the source-sink populations concept (Pulliam et al. 2000). Abiotic conditions can impact all plant species at any growth stage (i.e. seeds, germination stage and flowering stage) (Fig 1-9) (Bobbink et al., 2010). They can also alter the reproduction success and maturation, and even when the abiotic conditions are extreme, they may kill the established plant species preventing local persistence through the establishment of the next generation (Fig 1-9) (Walther et al., 2002; D. Wiens et al., 1987). It is often challenging to disentangle the effect of abiotic filtering and dispersal limitation since it usually requires experimental approaches, for example by introducing a given species in a target community to avoid dispersal limitation (approach adopted in **Chapters 3 & 4**). Alternatively, studying the soil seed bank composition within a given community at a given time in parallel

to assessing plant species composition of the focal community may help to identify plant species which overcame dispersal limitations but face recruitment limitations under current conditions.

It is well accepted that the presence of a plant species in a certain habitat depends on its tolerance to environmental stress and disturbance (Yuanzhi Li & Shipley, 2018). Habitats exhibiting harsh environmental conditions often host a low species richness (Fig 1-8B) (Begon, Townsend, & Harper, 2006). However, some species are able to withstand and even colonize sites despite extreme conditions (e.g. freezing temperatures, low pH, salinity and shortage of water and nutrients) (Begon et al., 2006; Van der Meulen, Hudson, & Scheiner, 2001). In this case, colonization, competitive success, tolerance and survival will trigger the dominance of one to few species, whilst other species will be unable to establish or will go extinct (Maestre, Callaway, Valladares, & Lortie, 2009; Michalet et al., 2006). As long as a plant community is facing harsh conditions, it will achieve low productivity levels (Fig 1-8B), eventually limiting alpha diversity (i.e. local species richness). A low alpha diversity is often associated with a low productivity because of resource shortening and physical stress (Adler, Seabloom, Borer, Hillebrand, Hautier, Hector, Harpole, O'Halloran, et al., 2011; Chesson & Huntly, 1997; Gillman & Wright, 2006). In addition, less productive sites are associated with less competition events and more facilitation relationships compared to more productive sites (Fig 1-8A). In the latter (non-harsh environmental conditions), competition for resources likely increases and community saturation may occur (chapter 2). Therefore, abiotic conditions affect the productivity of plant communities, which affects community structure, function and species composition.

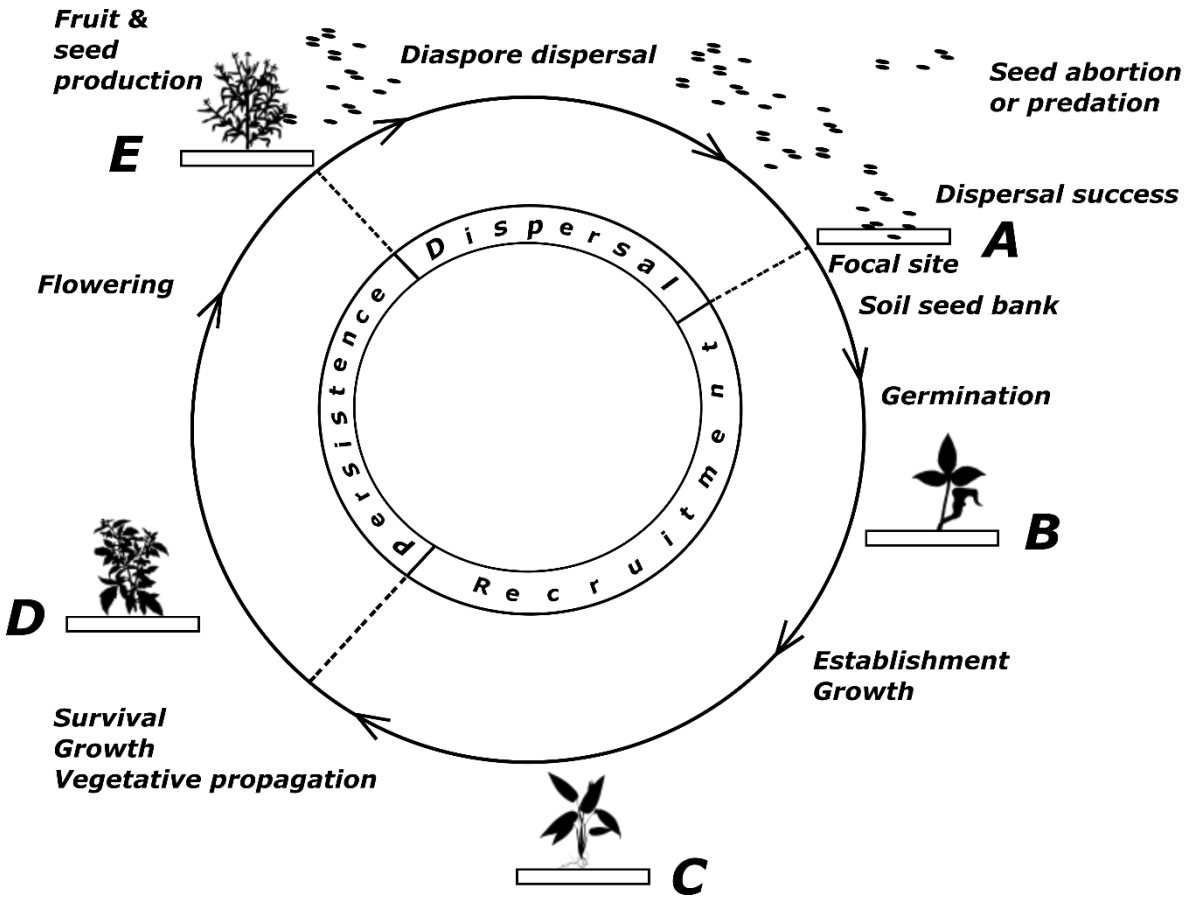

Figure 1-9: The plant life cycle *begins with a diaspore (seed, fruit, spore or vegetative propagule) which successfully reach a focal site by dispersal* ***(A)****. The diaspore will germinate and produce a tiny, immature plant (called seedling when coming from a seed)* ***(B)****. The seedling will establish and grow as long as environmental conditions are favorable* ***(C)****. A mature plant will form with higher survival rates and ability for vegetative propagation* ***(D)****. During the flowering stage of plant's lifecycle, diaspores will be produced via sexual or vegetative multiplication* ***(E)*** *allowing the beginning of a new life cycle.*

1.3.3. Biotic interactions

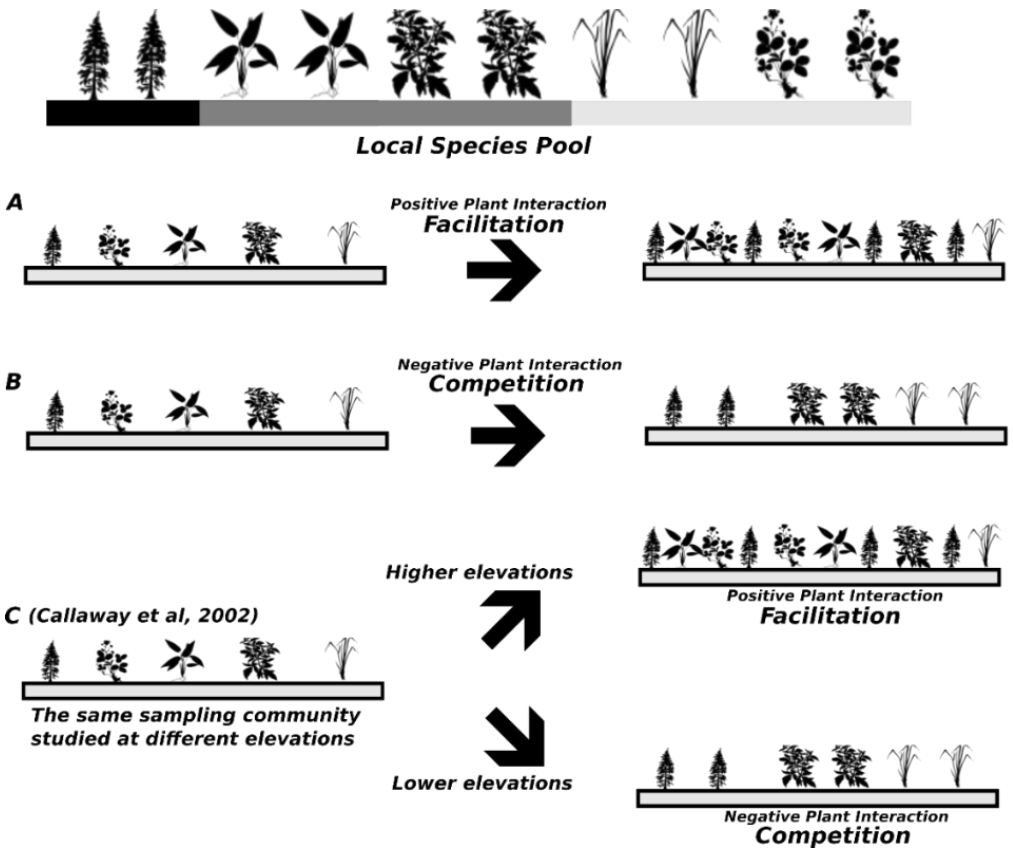

Figure 1-10: Biotic interactions occurring at the local scale. (A) *represents positive plant interactions (e.g. facilitation).* ***(B)*** *represents negative plant interactions (e.g. competition).* ***(C)*** *represents the study done by Callaway et al. (2002) showing that the interaction between species is also affected by abiotic factors (effect of elevation of species interactions). Inspired from Callaway et al (2002).*

Biotic interactions are thought to impact community structure after the community has been filtered by abiotic constraints, while the reality is that both biotic and abiotic factors may simultaneously and not independently affect plant species throughout their life cycle. Biotic interactions are those interactions that occur between plants themselves (cf. plant-plant interactions) and between plants and other organisms (animals, microbes) in a pattern that affects community assembly and thus community structure (Austin, 1985; R. W. Brooker, 2006; Michalet et al., 2006). Plant-plant interactions can be positive (e.g. facilitation) or negative (e.g. competition) (Fig. 1-10 & 1-1).

Positive interactions (i.e. facilitation) usually occur between neighboring and physiologically independent organisms (e.g. non-parasitic plants) (R. W. Brooker et al., 2008) (Fig. 1-10A & 1-1D). The neighboring species will protect plants from the consequences of extreme climatic episodes and pest invasion, enhance soil nutrient availability, provide a shelter or adequate microsite conditions such as modulated temperature and soil moisture (Bonanomi, Incerti, & Mazzoleni, 2011; R. W. Brooker et al., 2008; Muoghalu, 2009). An example of positive interactions is the presence of "nurse plants" that are species arising in hot and dry environments, and generate microclimatic conditions making it possible for other species to recruit. Therefore, facilitation plays a crucial role in determining the diversity and structure of plant communities.

Conversely, negative interactions among species and between plants and other organisms would reduce chances of establishment and survival in a particular community (Fig. 1-10B & 1-1E). Competition and the presence of natural enemies (e.g. parasites, herbivores) are considered important means by which plant communities are filtered (R. W. Brooker, 2006), where neighbouring plants and other species compete for nutrients, light and space (R. W. Brooker et al., 2008). In his "Competitive Exclusion Principle", Hardin, (1960) proposed a hypothesis stating that two competitors cannot coexist unless they have difference in their niche requirements (niche theory). Callaway et al. (2002) showed that the same plant species growing at different elevations shows different responses with respect of its interactions with neighbouring plants (Fig. 1-10C). In this study, plants grown at lower elevations showed negative interactions through competition, whereas those grown at higher elevations (harsher conditions) showed positive interactions through facilitation. Thus, both positive and negative biotic interactions may differ along a gradient of abiotic conditions, and thus influence differently community structure and species diversity.

1.3.4. Spatial scale and environmental heterogeneity

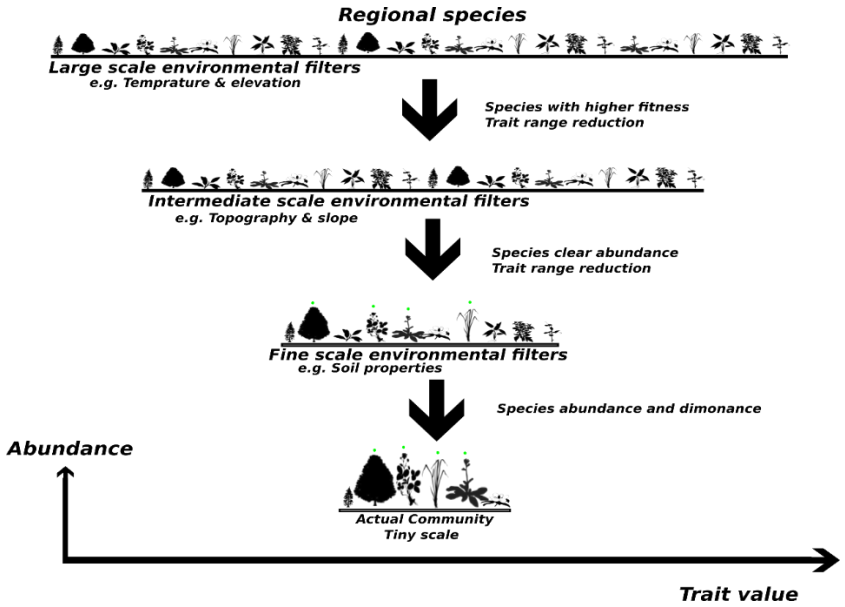

Figure 1-11: Nested filtering effects from large scale to the fine scale (extent community). *With reduced scale, species fitting the environmental conditions will increase their abundance and dominate (green dots). Therefore, both environmental filters and scale difference will illustrate the dissimilarity among species traits and decide the coexistence potential of species at the local scales. Inspired from de Bello et al. (2013).*

Scale dependency is not a recent challenge for ecologists. It has been proven to affect the means by which a community can be interpreted (Colwell & Winkler, 1984; Levin, 1992). The scale by which a community is studied clarifies the perception of the researcher towards the hypothesis proposal and the way by which results are interpreted (Fig 1-5) (Swenson, Enquist, Pither, Thompson, & Zimmerman, 2006). When dealing with small spatial scales, the interspecific and intraspecific interactions between species may drive the biotic filters which shape community structure at these small scales (Fig 1-5) (Stoll & Weiner, 2000). The impact of biotic filters on the neighboring species may range from few millimeters to one square meter (minimal scale studied in **Chapter 2**) for herbaceous species (less impact on trees and shrubs) (Fig 1-11). However, considering larger spatial scales (e.g. 1000 m^2) with their environmental gradients elucidates the importance of biotic interactions relative to abiotic conditions and

dispersal ability (Gotelli & McCabe, 2002; Watkins & Wilson, 2003). This can be applied when focusing on plant communities, while for other organisms (e.g. birds); it is more complex when studying the impact of biotic interactions at larger spatial scales.

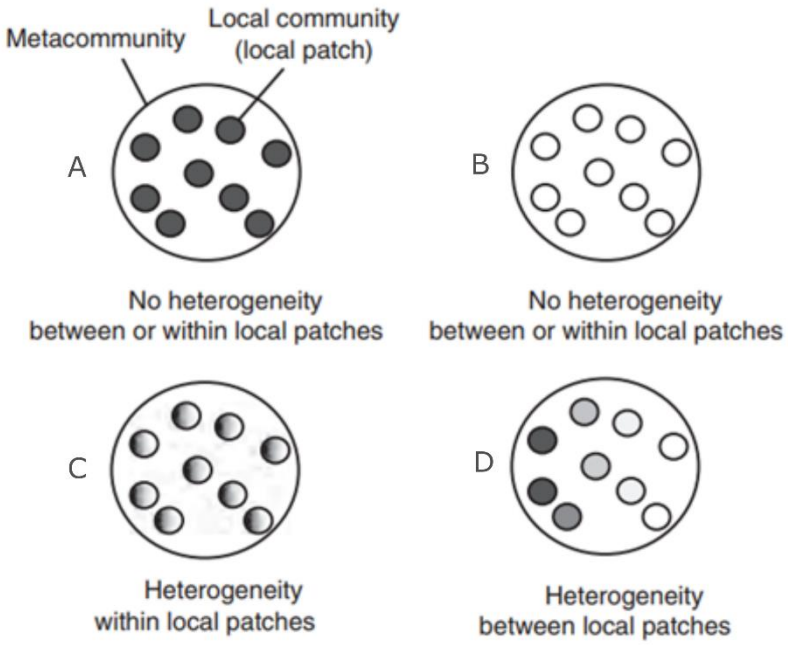

Figure 1-12: Different patterns of environmental heterogeneity. ***(A)*** *&* ***(B)*** *represent communities with no heterogeneity across their local patches.* ***(C)*** *represents communities showing heterogeneity within their local patches.* ***(D)*** *represents communities showing heterogeneity between their local patches. Extracted from (Fukami, 2010).*

Environmental heterogeneity, measured as the diversity of the available ecological niches in an ecosystem, is thought to determine species diversity and composition and the structure of plant communities (H. V. Cornell & Lawton, 1992a; David Tilman, 1999a). A study by Hutchinson (1961) predicted that, when habitat heterogeneity is at its maximum, species diversity reaches its highest values since each species is directed towards its compatible niche and competition will be minimal ("niche diversification hypothesis"). Shurin et al. (2004) conducted an experiment into which two competing species were introduced in multiple patches with different resource supply. The results showed that in case of patches having similar

resources, one of the species outcompetes the other species; but in case of patches varying in the resource ratio, one of the species dominates while the other still persist but as dominated species. This study clearly links the spatial scale to environmental heterogeneity in the context of community assembly, where species richness in the metacommunity is maximal when heterogeneity in environmental conditions occurs between (Fig. 1-12d) rather than within the local patches (Fig 1-12c) (B. M. Williams & Houseman, 2014).

It is therefore of great importance for ecologists studying community assembly to take into consideration what characterizes the community itself (i.e. heterogeneity), the plant species pool (i.e. spatial scale) and their interaction in determining community structure (Kneitel & Chase, 2004).

1.3.5. Stochastic processes vs. deterministic processes

Stochastic processes are the processes that lead to a random change in the local populations with time (Hanski, Gilpin, & McCauley, 1997). From an ecological time scale point of view, we can distinguish two stochastic processes that are believed to affect plant populations, namely demographic stochasticity and environmental stochasticity (Lande, 1993; Melbourne & Hastings, 2008). Demographic processes include species mortality and reproduction events that make population growth rates fluctuating randomly (Engen, Bakke, & Islam, 1998). Even if we assume equal reproduction and death rates for all individuals in the population (neutral theory), the number of offspring and the death time of every single individual is clearly unpredictable, which leads to random differences in species-specific population size. Environmental stochasticity encompasses processes that generate unpredictable changes in the environmental conditions, thereby leading to variations in population growth rates (Lande, 1993). Natural disturbances are examples of these processes that have the same effect on all species found in the community. Stochastic processes occur in all population regardless of their size, but they

are with greater impact in small populations (Pavlik, 1995; David Tilman, 2004). In case of random changes in the size of small populations, species are more exposed to local extinction (Hanski, 2001). In addition, the ability of species to disperse from nearby populations will be inhibited and the population tends to be more isolated.

Unlike stochastic processes, deterministic processes are those that lead to a predictable change in the population size (i.e. decline or rise) (Loreau et al., 2001a). Population size tends to decrease in case of habitat loss, where the availability of the resources decreases, leading to competitive events and to a decrease in the survival rates and reproduction (D. Goldberg & Novoplansky, 1997). Two deterministic processes are thought to play an important role for community structure: habitat degradation and habitat isolation (Fischer & Lindenmayer, 2007a). Habitat degradation is defined as the breakdown and loss of habitat qualities (resources and conditions) that are considered a prerequisite for population growth and expansion, and mainly occurs at the edges (Lindenmayer & Fischer, 2013). Edge effects (explained in **Chapter 2**) have a considerable impact on populations and communities by promoting a change in biotic conditions (habitat structure or microclimate) (Báldi, 1999), biotic interactions (species abundance, species invasion, interaction strength and quality) (R. J. Hobbs & Yates, 2003) or by increasing the negative impacts of anthropogenic disturbances (fire, hunting and domesticated animals) (Meiners & Pickett, 1999). Habitat isolation is believed to alter populations and communities when the dispersal ability of species is disrupted (Van Ruremonde & Kalkhoven, 1991). In this case, species are with more chances to disperse in the unsuitable matrix, and consequently with increased risk of mortality (Ricketts, 2001).

Species are exposed to extinction via stochastic or deterministic processes, both processes often acting together (Chase, 2010; Zambelli, Siqueira, Cicogna, & Soares, 2006). This is because, when deterministic processes take place, population size decreases, making it more vulnerable to stochastic processes (Bennett & Saunders, 2010). In addition, when one or

more species go extinct, this often leads to cascading deterministic effects (Soulé, Alberts, & Bolger, 1992). For example, when certain predators go extinct due to fragmentation, this will affect the lower trophic levels by increasing the abundance of prey species, which in turn will overconsume resources, leading to the disruption of ecosystem processes and increased vulnerability of other species (Ryall & Fahrig, 2006).

1.4. Objectives and thesis structure

The main objective of my PhD thesis was to study the relative importance of dispersal and recruitment limitations in shaping community structure by means of both field observations and experimental approaches. For this purpose, we used different model communities, ranging from anthropogenic habitats (i.e. croplands in intensive openfield landscapes) to semi-natural habitats (forest patches and hedgerows) acting as biological corridors within artificialized landscape matrices.

Chapter 2 is entitled "Forest fragmentation shapes the alpha-gamma relationship in plant communities". In this chapter, we used field observations to analyse the relationship between local richness (alpha diversity) and regional richness (gamma diversity) also coined the alpha-gamma relationship (AGR) or the local-regional relationship (LRR) in the scientific literature (Szava-Kovats, Ronk, & Pärtel, 2013; Cornell & Lawton, 1992). Patterns emerging from this relationship help to understand the main processes underlying community assembly (Connel & Lawton 1992). In chapter 2, we analysed the AGR for both forest specialists and generalists between different regions in Northern France (Hauts-de-France) differing in spatial resolution (species pool) and landscape context, i.e. non- (fake patches within a forest matrix), semi- (small, connected patches within a matrix of grasslands) and highly fragmented (small, isolated patches within a matrix of crop fields) systems. For this purpose, we used the most

recent scientific advances to analyse the AGR (i.e. the log-ratio model developed by Szava-Kovats, Ronk, & Pärtel (2013).

Chapter 3 is entitled "Winter cover crops decreases the abundance of weeds while increasing cash-crop yields". A major limit inherent to any empirical study comparing different agricultural techniques on weed communities is that the absence of a given weed is hardly interpretable: it may be either because seeds are not present (dispersal limitation) or because seeds do not germinate (recruitment limitation) or seedlings die rapidly after emergence and do not establish (recruitment limitation). By seeding the studied species directly in the field and by controlling propagule pressure, we overcome dispersal limitations. Then, we monitored both germination and seedling recruitment to assess whether recruitment limitations matter for weed species. Hence, if the seeded species germinate and establish successfully knowing that it would be absent if we did not seed the species, then we can conclude that dispersal limitations applies; if they are not retrieved, then recruitment limitations also applies in addition to dispersal limitations. Using vascular plant species as a model, we compared the effect of contrasted agricultural practices on a controlled weed community. These practices involve the presence/absence of permanent plant cover (in summer: sunflower; and/or in winter: Leguminosae or *Camelina sativa*), as an example of biotic filter; and tillage/reduced-tillage, as an example of abiotic filter (disturbance regime). We used a randomized complete block design with three replicates per treatment.

Chapter 4 is entitled "Hedgerows as corridors for forest plant species: a test for seed germination and plant establishment". Species that are specialist of forest habitats often are absent from recent hedgerows, but sometimes occur in ancient hedgerows. Since most forest specialists are dispersal-limited, their absence in recent hedgerows can be explained by a lack of dispersion rather than by recruitment limitations. Alternatively, recent hedgerows may provide forest specialists with sub-optimal environmental conditions (e.g. high soil phosphorus

content, unfavorable microclimate) or biotic factors (e.g. interspecific competition) so that those species may fail to recruit and persist even if they may disperse inside the recent hedgerows. We implemented a controlled experiment into which several forest plant species were sown (seed experiment to disentangle dispersal from germination limitations) and transplanted as adults (transplant experiment to test for establishment limitation) in recent hedgerows of controlled composition and structure. As this experiment is still ongoing and was recently initiated, we will only show very preliminary results. Once the full monitoring achieved, we should be able to explain the presence/absence of forest plant species in hedgerows and ultimately, to conclude on their potential function as ecological corridors for forest plant species.

Chapter 5 is a general discussion of the results obtained in the previous chapters. We will summarize the main achievements of this thesis, try to derive a general conclusion and provide future research perspective.

Chapter 2: Forest fragmentation shapes the alpha-gamma relationship in plant diversity

2.1. Résumé

Questions : Il est reconnue que la fragmentation forestière a un impact globalement négatif sur la richesse en espèces forestières à la fois aux échelles les plus locales (diversité α) comme aux échelles supérieures (diversité γ). Néanmoins, l'effet de la fragmentation forestière sur le couplage entre diversité α et γ n'a pas été étudié. Une des hypothèses sous-jacente est que la fragmentation de l'habitat favoriserait le découplage avec saturation de la diversité α (atteinte d'un plateau) à mesure que la diversité γ augmente ?

Lieu : Picardie.

Méthodes : Nous avons évalué la biodiversité en espèces végétales au sein de 116 fragments forestiers suivant un gradient à trois niveaux de fragmentation de l'habitat: aucune fragmentation (forêt continue) ; fragmentation intermédiaire (fragments forestiers reliées par un réseau de haies) ; et fragmentation élevé (fragments forestiers isolés au sein d'une matrice de champs cultivés). La richesse en espèces spécialistes de l'habitat forestier et en espèces plus généralistes a été étudiée à cinq résolutions spatiales emboîtées au sein de chaque fragment forestier: 1 m^2 ; 10m^2 ; 100m^2 ; 1000m^2 ; et superficie totale du fragment focal. Tout d'abord, nous avons utilisé le modèle proposé par Szava-Kovats, Ronk, & Pärtel (2013) permettant d'extraire le coefficient de pente qui résume de manière quantitative la forme de la relation α ~ γ. Nous l'avons fait séparément pour toutes les combinaisons possibles de niveau de fragmentation (aucun vs. intermédiaire vs élevé) × échelle spatiale (par exemple α-1m2 vs γ-10m2) × type d'espèce (par exemple α-spécialistes vs γ-spécialistes). Nous avons ensuite utilisé des modèles linéaires à effets mixtes pour analyser l'effet du niveau de fragmentation, de l'échelle spatiale, du type d'espèce et de tous les termes d'interaction d'ordre deux sur le

coefficient de pente extrait des modèles précédents (cf. modèle de Szava-Kovats, Ronk, & Pärtel (2013).

Résultats : L'analyse de la variation des coefficients de pente issus du modèle de Szava-Kovats, Ronk, & Pärtel (2013) nous a permis de mettre en évidence une interaction entre le niveau de fragmentation et le type d'espèce (spécialistes vs. généralistes), de telle sorte que pour les spécialistes forestières, la relation $\alpha \sim \gamma$ change à mesure que la fragmentation augmente, en passant d'une relation linéaire pour les situations non fragmenté à une relation de saturation avec atteinte d'un plateau lorsque le niveau de fragmentation est élevé. On observe une tendance opposée pour les espèces généralistes.

Conclusions : La fragmentation forestière affecte la relation $\alpha \sim \gamma$ en favorisant les espèces généralistes au détriement des espèces forestières spécialistes, avec des mécanismes contrastés pour ces deux guildes. À mesure que la fragmentation augmente, (i) les spécialistes forestiers passent d'un échantillonnage proportionnel avec couplage entre diversité α et diversité γ à une saturation des communautés, conséquence probable de limitations à la dispersion, tandis que (ii) pour les espèces généralistes, la fragmentation favorise le couplage entre diversité α et diversité γ, conséquence probable des effets de lisières en contexte très fragmenté.

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2.2. Article title

Forest fragmentation shapes the alpha-gamma relationship in plant diversity

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ABSTRACT

Questions: Forest fragmentation affects species richness at both local (i.e. α-diversity) and relatively large (i.e. γ-diversity) scales, but does it decouple α- from γ-diversity through a shift from proportional sampling (i.e. α-diversity linearly increases with γ-diversity) to community saturation (i.e. α-diversity reaches a plateau as γ-diversity increases)?

Location: North France.

Methods: We surveyed 116 forest patches at three levels of forest fragmentation: none (continuous forest); intermediate (forest patches connected by hedgerows); and high (isolated forest patches). Plant species richness of both forest specialists and generalists was surveyed at five nested spatial resolutions across each forest patch: $1m^2$; $10m^2$; $100m^2$; $1000m^2$; and total forest patch area. First, we ran log-ratio models to extract the slope coefficient summarizing, in a quantitative manner, the shape of the $\alpha \sim \gamma$ relationship. We did that separately for all possible combinations of fragmentation level (none *vs*. intermediate *vs*. high) × spatial scale (e.g. α-$1m^2$ *vs*. γ-$10m^2$) × species type (e.g. α-specialists *vs*. γ-specialists). We then used linear mixed-effect models to analyze the effect of fragmentation level, spatial scale, species type and all two-way interaction terms on the slope coefficient extracted from all log-ratio models.

Results: We found an interaction between fragmentation level and species type, such that forest specialists shifted from a linear to a curvilinear-plateau relationship at low and high fragmentation, respectively, while the opposite pattern was true for generalists.

Conclusions: Forest fragmentation affects the $\alpha \sim \gamma$ relationship by favoring generalist species over forest specialists, with contrasted mechanisms for these two guilds. As fragmentation increases, (i) forest specialists shift from proportional sampling towards community saturation, as a likely consequence of dispersal limitation while (ii) generalists shift from community

saturation towards proportional sampling, as a likely consequence of the increased edge effect, which promotes a biodiversity spillover effect along the edge-core gradient.

KEYWORDS

Community assembly, anthropogenic disturbances, alpha diversity, gamma diversity, dispersal limitations, habitat fragmentation, local-regional richness relationship, metacommunity dynamics.

RUNNING HEADLINE

The alpha-gamma relationship in fragmented forests.

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ARTICLE TYPE

Research article

2.3. Introduction

Habitat loss and fragmentation (i.e. the breakdown of large and contiguous habitats into smaller and more isolated patches) is widely acknowledged as a major cause of biodiversity loss (D. Tilman, 2004; Wilcox & Murphy, 1985) having an impact on ecosystem functioning through the biodiversity-ecosystem-functioning (BEF) relationship (N. M. Haddad et al., 2015; Riitters, Wickham, Neill, Jones, & Smith, 2000). Many empirical and theoretical studies have investigated the effects of habitat loss and fragmentation on species richness at different spatial scales from local (i.e. α-diversity) to larger (i.e. γ-diversity) scales (Baynes et al., 2016; Carrara et al., 2015; Fahrig, 2013a; Hanski, 2015; Riitters et al., 2000; Rybicki & Hanski, 2013; Valdés et al., 2015) through intermediate scales (i.e. β-diversity) (Arroyo-Rodríguez et al., 2013; Baselga, 2010; Noss, 1983). A decrease in habitat patch size results in lower species richness due to both direct and stochastic area-dependent extinction (Few, Ahern, Matthies, & Kovats, 2004; Pimm, Jones, & Diamond, 1988). Increased habitat patch isolation reduces migration among local communities and magnifies dispersal limitations, thereby impeding metacommunity processes (e.g. rescue and mass effects; Leibold et al., 2004) and ultimately reducing species richness of all habitat patches (Jamoneau, Chabrerie, Closset-Kopp, & Decocq, 2012). Moreover, the increase in the edge:core ratio following fragmentation alters habitat quality, which has been shown to be particularly detrimental to habitat specialists (Mortelliti et al., 2011). *Per contra*, generalist species originating from the surrounding landscape may benefit from an increase in the edge:core ratio, thereby altering species richness within the habitat patches (Hanski, 2015; Vandermeer & Carvajal, 2001). Habitat fragmentation *per se* (i.e. the breaking apart of habitat after controlling for habitat loss) (Fahrig, 2003) and management of the landscape matrix may thus alter the relationship between α- and γ-diversity (*sensu* Belote, Sanders, & Jones, 2009; Cornell & Lawton, 1992; Starzomski, Parker, &

Srivastava, 2008). But surprisingly, how fragmentation impacts this $\alpha \sim \gamma$ relationship – and potentially decouples α- and γ-diversity – has received little attention so far.

Local species assemblages result from the interaction between local processes (e.g. competition, disturbance) and processes operating at relatively broad scales (e.g. dispersal) (Ricklefs, 1987). The relative importance of these two processes and the spatial scale at which they operate are commonly investigated by regressing α- against γ-diversity (Harrison & Cornell, 2008; He, Gaston, Connor, & Srivastava, 2005; Hillebrand & Blenckner, 2002; Leibold et al., 2004), hereafter referred as the $\alpha \sim \gamma$ relationship (AGR). A positive linear relationship indicates that the local community proportionally samples the set of species available at a larger spatial extent (i.e. the number of species present in a larger area determines the local community: α- and γ-diversity are coupled), whilst a curvilinear-plateau relationship reflects community saturation (i.e. local species interactions limit the number of species that can locally coexist: α- and γ-diversity are decoupled) (Cornell & Lawton, 1992; Srivastava et al., 2008). However, these patterns have been shown to depend upon environmental severity/stress, with community saturation being predominant under both benign and severe environmental conditions, while proportional sampling dominates under intermediate positions along the environmental severity gradient (Michalet et al., 2015). Since fragmentation can also be considered a stress, we might expect a similar influence of fragmentation on the AGR. Moreover, the AGR may also change in the course of forest succession, with pseudo-saturation (*sensu* Lawton and Strong (1981)) in early stages due to the quick colonization of good dispersers, unsaturation at intermediate stages and saturation in late-successional stages following competitive exclusion (Srivastava et al., 2008).

Forest patchiness is not only the result of fragmentation *per se*, but also the result of the afforestation of former agricultural lands at different times (Herault & Honnay, 2005). Forest fragmentation may thus not only happen under stable (no habitat loss) forest cover conditions

but even under forest gain (Estreguil, Caudullo, de Rigo, & San-Miguel-Ayanz, 2013). This means that total species richness within the landscape does not necessarily decrease with an increasing level of fragmentation (Hanski, 2015). In fact, it may even increase as fragmentation increases until the level of fragmentation reaches a threshold that is detrimental to biodiversity as a whole such that total species richness in the landscape decreases. To illustrate this, consider a set of local sites or plots located in virtual forest patches within a continuous forest matrix (Fig. 1, left panel). Plant community composition within these plots chiefly consists of forest specialists (FS), i.e. species that are more or less restricted to closed-canopy forest as habitat (Carrara et al., 2015; Schlinkert et al., 2016; Valdés et al., 2015). Now, consider a set of plots located in true forest patches with similar sizes and shapes as in the previous example but connected together by linear woody elements (e.g. hedgerows) within a matrix dominated by grasslands (Fig. 1, central panel). Then, forest generalists (FG), i.e. species that have their optimum in open habitats but may survive forest conditions (Valdés et al., 2015), are likely to enter the forest patches and co-occur with forest specialists, thereby increasing the number of species co-occurring within the same forest patches compared with the situation in the non-fragmented forests. Finally, if we disconnect the same forest patches and place them within a matrix of intensively cultivated croplands (Fig. 1, right panel), we expect a negative effect primarily on forest specialist species, and ultimately on generalist species, by boosting extinction cascades and by limiting immigration (Fischer & Lindenmayer, 2007) so that the number of species co-occurring within the forest patches will drop.

The pure effect of fragmentation on the AGR will depend upon the balance between colonization and extirpation events that happen at both the local plot scale and the larger forest patch scale. Colonization events of a new plant species not yet occurring within a given forest patch will first happen at the scale of the forest patch before it can happen at the plot scale of local assemblages inside the forest patch (e.g. a generalist species likely entering the patch

through the edge). *Per contra*, extirpation events of a given plant species will occur faster at the local plot scale than at the entire forest patch scale (e.g. local extirpation of a forest specialist). These processes are predicted to be more pronounced in small forest patches and/or within intensively managed agricultural landscapes because of stronger edge effects (e.g. increased light and nutrient levels) which favor generalist plant species at the expense of forest plant specialists (Bossuyt, Heyn, & Hermy, 2000; Michalet et al., 2015; He et al., 2005). Based on these considerations, we predict a shift from proportional sampling (i.e. α-diversity is coupled to γ-diversity and increases linearly as γ-diversity increases) to community saturation (i.e. α-diversity is decoupled from γ-diversity and reaches a threshold as γ-diversity increases) for forest plant specialists as the level of fragmentation increases (see before last row in Fig. 1) while the opposite pattern is expected for forest generalists (see last row in Fig. 1). In addition to this interaction effect between the fragmentation level and species type, we also assume different shapes of AGR for specialists and generalists depending on the difference in spatial resolution between α- and γ-diversity, with community saturation more likely to occur when this difference is large (Loreau, 2000).

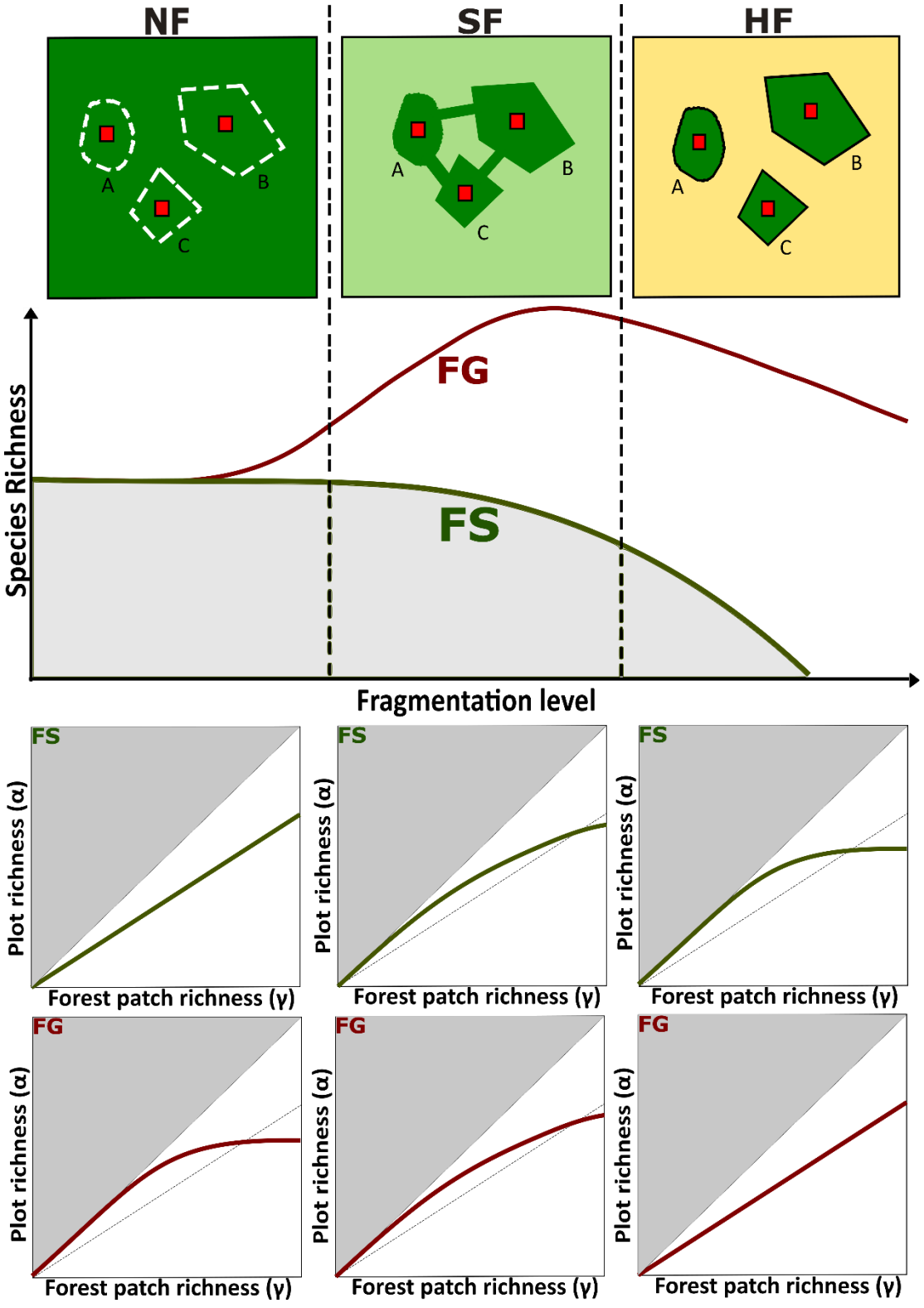

Figure 2-1: Schematic Schematic figure of the expected effect of forest fragmentation *(none, intermediate and high) on the shape of the $\alpha \sim \gamma$ relationship (AGR) for forest specialists (FS) and generalists (FG). For FS in non-fragmented (NF) systems, we expect proportional sampling patterns (Type I) (i.e. α-diversity increases linearly as γ-diversity increases) to*

predominate while in highly-fragmented (HF) systems, we expect FS to display a predominance of curvilinear-plateau patterns (Type II) (i.e. α-diversity increases until reaching a plateau as γ-diversity increases). For FG, we expect the exact opposite situation as fragmentation increases. In the case of semi-fragmented (SF) systems, where both FS and FG species may locally co-occur, we expect intermediate or even indeterminate patterns to predominate for both FS and FG. For illustrative purpose, three forest patches (A, B and C), being connected or not by corridors (e.g. hedgerows), are depicted within three different types of matrices (forest, pastures with hedgerows, croplands). The less disturbed matrix is a forest matrix with continuous forest patches depicted by the white dotted lines while the most disturbed matrix is an agricultural landscape of croplands with forest patches being isolated from each other. The intermediate matrix is a matrix of pastures with forest patches being connected by hedgerows. The red squares inside the forest patches represent α-diversity while the total patch area represents γ-diversity.

2.4. Materials and Methods

2.4.1. Study area

The study area is located in North France (N49°25'–50°11'; E1°52'–3°55'; alt. 60–220m) (Fig. 2). The climate is oceanic with a mean annual temperature of 10°C and total annual rainfall of 700mm. The geological substrate is dominated by Cretaceous chalks, usually covered by Quaternary loess. The study region is dominated by croplands, intensively cultivated for cereals, rapeseed and sugar beet: the so-called "openfield" landscape. The forest cover is highly fragmented, consisting of small, more or less remote forest patches. In some areas, the forest cover is also fragmented, but forest patches are more or less connected by hedgerows and the use of agrochemicals is lower than in the openfield landscape: this is the so-called "bocage" landscape. Large and "non-fragmented" forests, that are often former royal forests, are rare across the study region.

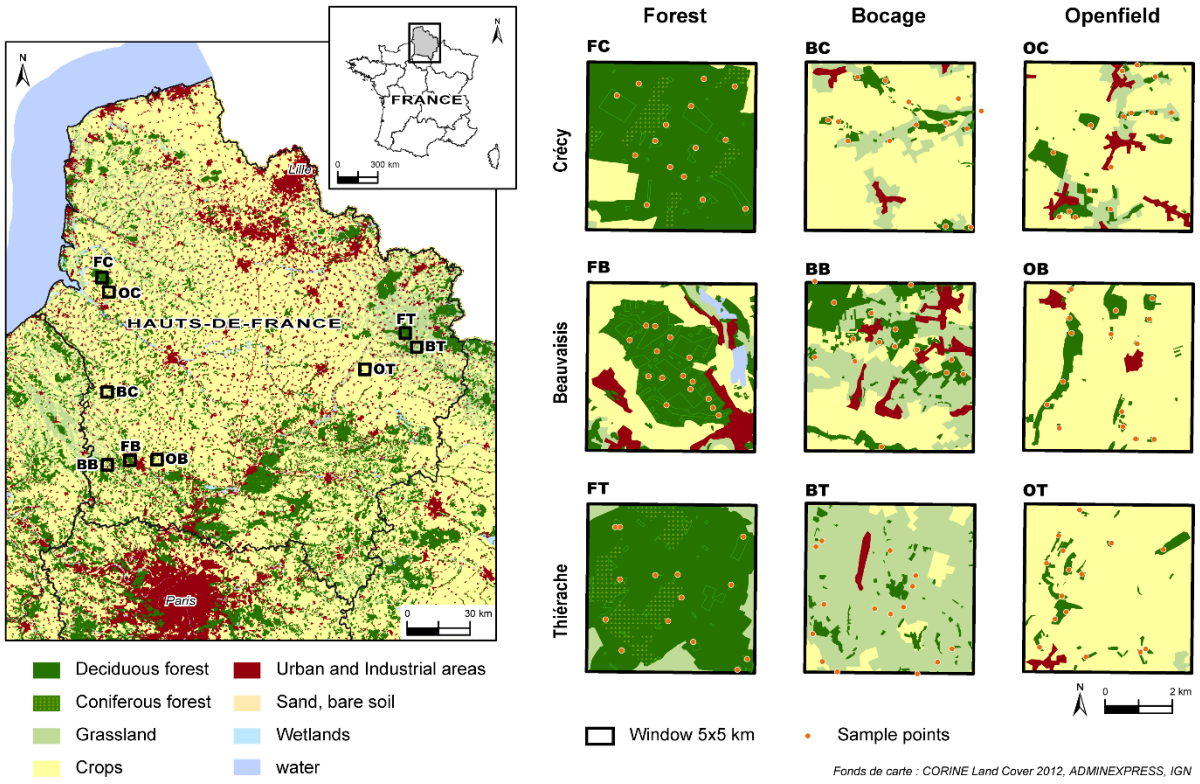

Figure 2-2: Map of the study area (North France) covering three different regions *(C: Ponthieu and Oise normande, B: Pays de Bray and Beauvaisis, T: Thiérache and Vermandois)*

with three different types of habitats (Forest, Bocage, Openfield), totaling nine landscape windows with 15 quadrats per window (n = 135 quadrats). Each quadrat is a set of four spatial resolutions, in addition to total patch area, nested within each other: 1m^2; 10m^2; 100m^2; and 1000m^2.

2.4.2. Study design and vegetation survey

We selected three replicates of 5km × 5km landscape windows in all three above-mentioned contrasted types of landscape (Fig. 2): (1) non-fragmented forests (NF), into which we created virtual forest patches (see Jamoneau, Chabrerie, Closset-Kopp, & Decocq, (2012) for more details on how virtual forest patches were delineated in the landscape), that mimicked the number, size and shape of the true forest patches found in the two other windows of the same set; (2) bocage or semi-fragmented forests (SF), consisting of small forest patches embedded in a grassland-dominated matrix and connected by hedgerows; and (3) openfield or highly-fragmented forests (HF), where the forest habitat consisted of small, isolated forest patches surrounded by intensively cultivated croplands. In each of the nine landscape windows, we randomly selected 15 forest patches with sizes and shapes allowing us to set up a 1000m^2 quadrat at the core of the forest patch so that the closest forest edge was located at a minimum distance of 10m. Whenever a window had less than 15 forest patches meeting these criteria, several non-overlapping quadrats (two to four) were arranged within the same large forest patch. A total of 135 quadrats (9 windows × 15 quadrats) were installed across 116 forest patches, including 39, 36 and 41 forest patches in NF, SF and HF systems, respectively (see raw data in Appendix 2-1).

Between 2007 and 2008, all 116 forest patches were visited twice, in spring (April–May) and in summer (June–September): we walked along parallel transects located 10m apart from each other to record all vascular plant species. We thus obtained a value of species richness per forest patch, i.e. patch-scale diversity. In addition to patch-scale diversity, specific floristic surveys were carried out at four nested spatial resolutions within each of the 135 quadrats of

1000m^2, using a logarithmic nested-plot design (see Fig. 1c in Wasof et al., (2018)): 1m^2; 10m^2; 100 m^2; and 1000m^2.

We focused on vascular plant species occurring within the herbaceous layer (height < 1m) solely as it better reflects spontaneous vegetation than in the shrub (height from 1 to 8m) and tree (height > 8m) layers which are more dependent on forest management practices. Intraspecific taxa and planted ornamentals were omitted. Taxonomic agglomerates (e.g. *Rubus fruticosus* agg., *Taraxacum officinale* agg.) were treated as single species. Finally, each of the 175 herbaceous plant species recorded across our study area was classified as either a forest specialist (FS: n = 43) or a forest generalist (FG: n = 132) (see Appendix 2-2).

2.4.3. Patch characteristics, habitat quality and the proportion of forest within the landscape

To correct for the effects of patch characteristics (area, length and age), habitat quality (soil and light conditions) and the amount of habitat around the focal forest patch (proportion of forest habitat within the landscape) on the AGR, we prepared several variables (Appendix 2-3) to be included as covariates in all the log-ratio models we ran (see next subsection entitled "Data analysis"). Including these covariates in the log-ratio models allowed us to determine the shape of the AGR for different levels of fragmentation, scale and species type, but independently from potential confounding effects due to differences in patch size, patch age, patch quality and forest loss or gain in the surrounding landscape (here we are interested in the pure effect of habitat fragmentation and not in habitat loss or gain which may confound with habitat fragmentation *per se*).

2.4.4. Data analysis

To test our hypotheses, we used a two-step modelling approach. First, we had to assess the shape of the AGR for all possible combinations of fragmentation level (NF, SF, HF) × spatial scale (e.g. α-1m^2 *vs*. γ-10m^2) × species type (e.g. $\alpha_{FS} \sim \gamma_{FS}$), while controlling for the effect of

several covariates (Appendix 2-3). Like in Belote et al. (2009), we considered species richness of any spatial resolution nested within a larger one as α-diversity relative to the species richness in the larger plot which we considered as γ-diversity. This leads to a total of ten combinations of nested spatial scales: (1) α-1m^2 *vs*. γ-10m^2; (2) α-1m^2 *vs*. γ-100m^2; (3) α-1m^2 *vs*. γ-1000m^2; (4) α-1m^2 *vs*. γ-total; (5) α-10m^2 *vs*. γ-100m^2; (6) α-10m^2 *vs*. γ-1000m^2; (7) α-10m^2 *vs*. γ-total; (8) α-100m^2 *vs*. γ-1000m^2; (9) α-100m^2 *vs*. γ-total; and (10) α-1000m^2 *vs*. γ-total. Regarding species type, we not only considered FS and FG separately when analyzing the AGR but we also considered the total diversity (FS+FG) to be able to test whether distinguishing between FS and FG changed the effect of forest fragmentation on the shape of the AGR compared to a baseline situation which does not distinguish between both species types. This leads to a total of three possible relationships that we tested: (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$; (2) $\alpha_{FS} \sim \gamma_{FS}$; and (3) $\alpha_{FG} \sim \gamma_{FG}$.

To assess the shape of the AGR, we ran a multiple-regression version of the log-ratio model proposed by Szava-Kovats, Zobel, and Pärtel (2012) (Equation 1) for each landscape window separately, for a given nested spatial scale combination (e.g. α-1m^2 *vs*. γ-10m^2) and for a given combination of species type relationship (e.g. $\alpha_{FS} \sim \gamma_{FS}$). This makes a total of 270 log-ratio models: three fragmentation levels × three replicates per fragmentation level × ten nested spatial scales × three species type relationships. The log-ratio model allows circumventing most statistical issues related to the traditional model (Cornell & Lawton, 1992) and especially the lack of statistical independence between α- and γ-diversity arising from the mathematical constraint that α is a subset of γ (R. C. Szava-Kovats, Ronk, & Pärtel, 2013b)

$$\ln\left(\frac{\alpha_i}{\gamma_i - \alpha_i}\right) = a + b\ln(\gamma_i) + \beta_1 Z_{1,i} + \beta_2 Z_{2,i} + \cdots + \beta_k Z_{k,i} + \varepsilon_i$$

Equation 1

According to equation 1, which accounts for the potential confounding effects of covariates (Z_k) and for which the response variable is the log-ratio of α- and γ-diversity values of a given quadrat *i*, the significance of the slope parameter *b* in front of the the log-transformed variable of γ-diversity allows to test whether the AGR significantly deviates from zero and thus from proportional sampling (linear or Type I curve) (Fig. 3). However, it does not allow to clearly distinguish between community saturation (curvilinear-plateau or Type II curve) and intermediate patterns between Type I and Type II curves (Szava-Kovats, Ronk, & Pärtel, 2013). To clearly distinguish between Type I, Type II and intermediate curves, we computed the 95% confidence interval (p-value < 0.05) around the estimated slope parameter *b* as proposed by Szava-Kovats et al. (2013). Based on the range of the confidence interval, we can distinguish between four cases (see Fig. 3c): Type I (the confidence interval includes 0 but not -1); Type II (the confidence interval includes -1 but not 0); intermediate (the confidence interval includes neither 0 nor -1); and indeterminate (the confidence interval includes both 0 and -1). The inverse transformation (Equation 2) of equation 1 allows drawing these curves in the original α ~ γ bi-dimensional space (Fig. 3b).

$$\alpha_i = \gamma_i \left(\frac{e^{a+b\ ln(\gamma_i)+\beta_1 Z_{1,i}+\beta_2 Z_{2,i}+\cdots+\beta_k Z_{k,i}+\varepsilon_i}}{1+e^{a+b\ ln(\gamma_i)+\beta_1 Z_{1,i}+\beta_2 Z_{2,i}+\cdots+\beta_k Z_{k,i}+\varepsilon_i}} \right)$$

Equation 2

To fit our data to equation 1, we used linear regression models with log(α/(γ-α)) as the response variable and log(γ) as the main predictor variable while accounting for several covariates (Equation 3): patch *area*, *length* and *age*; soil *pH*, *C:N* and *P*; *light* conditions (SCA); and the proportion of forest within a 500-m radius (*for500*) (see Appendix 2-3 for more information on the covariates). All covariates were standardized prior to analysis, i.e. the value for each variable was subtracted from its mean and divided by its standard deviation (Schielzeth, 2010).

$$\ln\left(\frac{\alpha}{\gamma-\alpha}\right) \sim \ln(\gamma) + area + length + age + pH + C{:}N + P + light + for_{500}$$

Equation 3

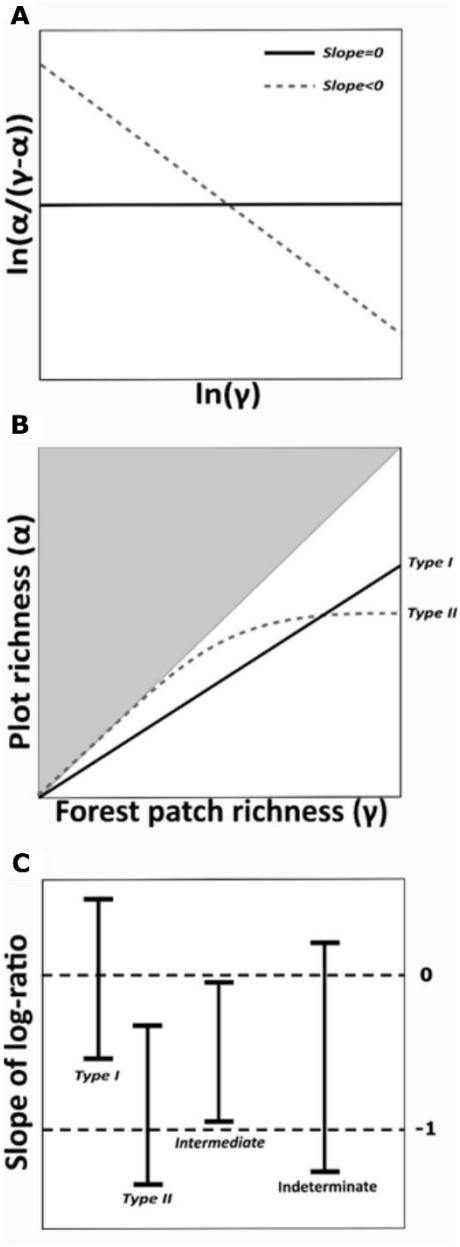

Figure 2-3: Schematic diagram of the different types of $\alpha \sim \gamma$ relationship (AGR) *that can be derived from the coefficient estimate or slope parameter of the log(γ) variable that we extracted from the log-ratio model (see Equation 1 in the main text). Slope values may be either close to and not significantly different from zero (black bold line) or significantly lower than zero (grey dotted line) in the log scale* ***(A)*** *showing either linear (Type I) or curvilinear (Type II) pattern in the natural scale (see Equation 2 in the main text to switch from the log scale to the natural scale)* ***(B)****, respectively. Based on the 95% confidence interval of each slope value, four*

different patterns may appear: Type I (the confidence interval includes 0 but not -1); Type II (the confidence interval includes -1 but not 0); intermediate (the confidence interval includes neither 0 nor -1); and indeterminate (the confidence interval includes both 0 and -1) ***(C)***.

Once the 270 log-ratio models were fitted, we extracted the slope coefficient (with the upper and lower limits of the corresponding 95% confidence interval) of log(γ), which provide a quantitative estimate of the shape of the AGR (Fig. 3). Then, we split the 270 slope coefficients into two different datasets: (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90) and (2) $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ (n = 180). For both datasets, we built several candidate models (i.e. step 2 in our analyses) to explain the observed variation in the *slope* coefficient (i.e. the response variable) extracted from the log-ratio models (i.e. step 1 in our analyses). As explanatory variables, we tested the effect of fragmentation level (*frag*: NF, SF, HF), spatial scale (*scale*: 1, 2, 3, 4), species type (*sp*: FS *vs*. FG) as well as all possible two-way interactions between all three variables. More specifically, we tested eight candidate models: (1) *slope ~ frag + sp*; (2) *slope ~ frag + scale*; (3) *slope ~ frag × sp*; (4) *slope ~ frag × scale*; (5) *slope ~ frag + scale + sp*; (6) *slope ~ frag × sp + scale*; (7) *slope ~ frag × scale + sp*; and (8) *slope ~ frag + scale × sp*. Spatial scale was here treated as a quantitative variable measuring the nestedness factor between α- and γ-diversity (e.g. α-1m^2 *vs.* γ-10m^2 and α-1m^2 *vs.*γ-100m^2 have nestedness factor of 1 and 2, respectively). Note that for the first dataset ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$), which focuses on all herbaceous plants without distinguishing between specialists and generalists, we could only test the effect of fragmentation level, spatial scale and the interaction between the two, thus leading to two candidate models only (*slope ~ frag + scale vs. slope ~ frag × scale*). To run our candidate models with the slope of the log-ratio models as the response variable, we used a linear mixed-effects modelling (LMM) approach with the three replicates per fragmentation level as well as the ten combinations of nested spatial resolutions as random intercept terms. To compare candidate models with nested fixed effects (but with the same random structure), we used

maximum likelihood (ML) estimation instead of restricted maximum likelihood (REML) (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). As the best candidate model, we selected the model with the smallest Akaike information criteria (AIC) and rerun the selected best model using REML for final inference and reporting of the models' parameters (Zuur et al., 2009).

All statistical analyses were performed using the "lme4" (Bates, Mächler, Bolker, & Walker, 2015), "nlme" (Pinheiro, 2002), "broom" (D. Robinson, 2014), "MuMIn" (Grueber, Nakagawa, Laws, & Jamieson, 2011), "glmm" (Green & MacLeod, 2016), "mvtnorm" (Genz & Bretz, 2009), "digest" (Genz & Bretz, 2009) and "Matrix" (Fiske & Chandler, 2011) packages in the R software environment version 3.4.1 (R Core Team 2017).

2.5. Results

In general, we found a clear predominance of Type I (i.e. linear) curves in the $\alpha \sim \gamma$ relationship (AGR) of herbaceous forest plants (Table 1). Focusing on the 90 slope values (mean ± standard deviation: -0.11 ± 0.22) (Fig. 4a) of the log-transformed variable of γ-diversity extracted from the 90 log-ratio models based on all herbaceous species, combining forest specialists with generalists at both the α and γ resolutions ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$), the best model (*slope* ~ *frag* + *scale*) showed a significant effect of fragmentation but no effect of spatial scale on the shape of the AGR (Table 2, see Appendix 2-4 for the output of other candidate models). Accordingly, the AGR shifted from a linear (Type I) to a curvilinear (Type II) pattern as the level of fragmentation increased (Fig. 4a and Fig. 5a). For the 180 slope values (0.02 ± 0.68) extracted from the 180 log-ratio models relating α to γ diversity of either forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) (n = 90) (Fig. 4b) or generalists ($\alpha_{FG} \sim \gamma_{FG}$) (n = 90) (Fig. 4c), we found a significant interaction effect between fragmentation and species type but no effect of spatial scale (best model: *slope* ~ *frag* × *sp*) (Table 2, see Appendix 2-4 for the output of other candidate models). The AGR of forest specialists showed a predominance of Type I and Type II curves in non-fragmented and highly-fragmented systems, respectively, while the AGR of forest generalists showed the complete opposite pattern; shifting from Type II to Type I as the fragmentation level increased (Table 1 and Figs. 5b and 5c).

Table 2-1: Based on the coefficient estimate or slope parameter of the log(γ) variable *(see Equation 1 in the main text) extracted from each of the 270 log-ratio models we ran (see main text for further explanations on the log-ratio models), the α ~ γ relationship (AGR) was classified into four types (I, II, INT, IND) for each of the three levels of fragmentation we tested (NF: non-fragmented; SF: semi-fragmented; HF: highly-fragmented) and for each of the three possible combinations of AGR we tested:* ***(1)*** $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ *(n = 90);* ***(2)*** $\alpha_{FS} \sim \gamma_{FS}$ *(n = 90); and (3)* $\alpha_{FG} \sim \gamma_{FG}$ *(n = 90). Acronyms I, II, INT and IND refer to Type I (proportional sampling), Type II (community saturation), intermediate and indeterminate curves, respectively (see main text for more information).*

(1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$				
	I	**II**	**INT**	**IND**
NF	17	2	6	5
SF	11	4	10	5
HF	14	12	2	2
Total	42	18	18	12
(2) $\alpha_{FS} \sim \gamma_{FS}$				
	I	**II**	**INT**	**IND**
NF	14	2	9	5
SF	8	7	11	4
HF	5	10	9	6
Total	27	19	29	15
(3) $\alpha_{FG} \sim \gamma_{FG}$				
	I	**II**	**INT**	**IND**
NF	4	15	6	5
SF	9	4	8	9
HF	13	4	8	5
Total	26	23	22	19

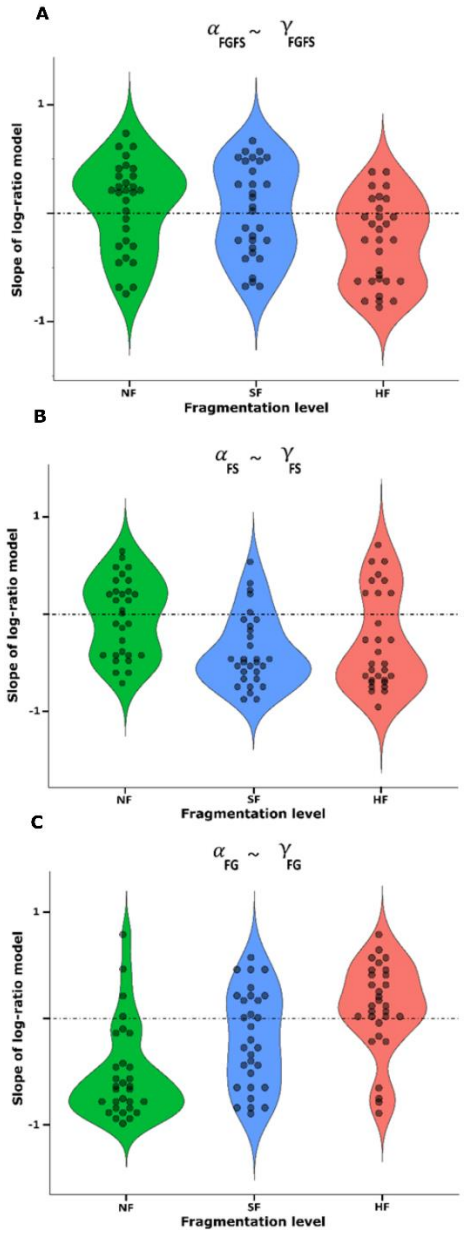

Figure 2-4: Variation in the distribution of the coefficient estimate or slope parameter of the log(γ) variable that we extracted from the log-ratio model *(see Equation 1 in the main text) and that we used to quantitatively assess the shape of the $\alpha \sim \gamma$ relationship (AGR). Panel* ***(A)*** *represents the distribution of the slope parameter for the combined pool comprising both forest specialists and generalists ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$). Panels* ***(B)*** *and* ***(C)*** *represent the distribution of the slope parameter, separately, for forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) and generalists ($\alpha_{FG} \sim \gamma_{FG}$), respectively. The FS, FG, NF, SF and HF acronyms refer to forest specialists, forest generalists, non-fragmented systems, semi-fragmented systems and highly-fragmented systems, respectively. Green, blue and red colors represent non-fragmented systems, semi-fragmented systems and highly fragmented systems, respectively.*

2.6. Discussion

Even after accounting for forest patch characteristics, habitat quality and the proportion of forest habitat within the landscape, the shape of the $\alpha \sim \gamma$ relationship (AGR) summarized by the slope parameter of the log-ratio model (Fig. 3) still varies a lot (Fig. 4), albeit proportional sampling seems predominant (slope values from the log-ratio models close to 0 in Fig. 4). This variability underlies complex interplays between the level of forest fragmentation and the degree of herbaceous species specialization for forests (Fig. 5). Although the AGR only describes patterns, these patterns may underlie important ecological processes (e.g. community saturation suggests biotic interactions or dispersal limitations) (He et al., 2005) that differ between forest specialists and generalists in response to forest fragmentation. Below, we discuss our main findings in light of the potential underlying ecological processes and their relevance for biodiversity conservation and landscape planning.

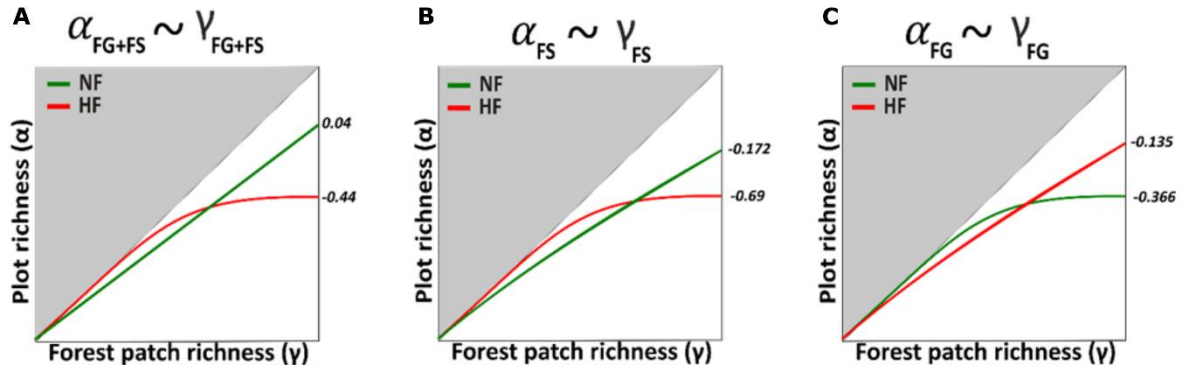

Figure 2-5: Changes in the $\alpha \sim \gamma$ relationship (AGR) as a function of fragmentation level*. Panel* ***(A)*** *represents the AGR of the combined pool comprising both forest specialists and generalists ($\alpha_{FS+FG} \sim \gamma_{FS+FG}$) showing linear (slope = 0.04) and curvilinear-plateau (slope = -0.44) AGR in non- and highly-fragmented systems, respectively. Panels* ***(B)*** *and* ***(C)*** *represent the AGR for forest specialists ($\alpha_{FS} \sim \gamma_{FS}$) and generalists ($\alpha_{FG} \sim \gamma_{FG}$), separately, with opposite patterns between the two guilds when shifting from non- to highly-fragmented systems. The FS, FG, NF and HF acronyms refer to forest specialists, forest generalists, non-fragmented systems and highly fragmented systems, respectively. Colors and drawings in Figure 5 (i.e. main results) mirror those used in Figure 4.*

Proportional sampling predominates but it hides complex interactions

In general, we found a predominance of linear (i.e. proportional sampling or Type I) AGR (Table 1), irrespective of the spatial resolution considered (Table 2), thus supporting former conclusions on the importance of regional processes in shaping local species richness (Cornell & Harrison, 2013; Harrison & Cornell, 2008). Yet, we also found that the prevalence of community saturation was the highest under some circumstances: for forest specialists within highly-fragmented systems and for generalist species within non-fragmented systems. This supports more recent findings on the relative importance of local processes under some environmental circumstances (Michalet et al., 2015). The critical analyses of Gonçalves-Souza, Romero, and Cottenie (2013) and Szava-Kovats et al., (2013), who used the log-ratio method to reanalyze data from 113 and 100 published datasets, respectively, found no prevalence of either unsaturated or saturated communities. In fact, these two meta-analyses concluded that a large proportion of studies produced no discernible patterns (i.e. intermediate and indeterminate cases). Accordingly, our results also show that intermediate and indeterminate patterns between Type I and Type II can contribute a significant proportion in the observed AGR, being predominant in semi-fragmented systems (Table 1). Overall, this suggests a gradual shift from either proportional sampling to community saturation (i.e. for forest specialists) or the opposite (i.e. for generalists) as the fragmentation level increases, thus supporting our initial hypothesis of a complex interplay between forest fragmentation and species type (Fig. 1).

Forest fragmentation negatively impacts forest specialists

Supporting our initial hypothesis for forest specialists (Fig. 1), we found a shift from proportional sampling within non-fragmented systems towards community saturation within highly-fragmented systems (i.e. isolated forest patches within a highly-disturbed matrix of croplands) (Fig. 5b), irrespective of the spatial resolution at which α and γ diversity are measured. Within non-fragmented forests, habitat quality is optimal and thus dispersal and recruitment limitations are low for forest specialists. Hence, a proportional increase in the

number of forest specialist species co-occurring locally can be observed with the increasing number of forest specialists available from a relatively larger area.

Per contra, highly fragmented forests negatively affect the local establishment of forest specialists, thus decreasing the slope value of the log-ratio model towards community saturation. First, this may reflect a relative increase in competitive exclusion, especially asymmetric competition, when more successful herbaceous plant species gain a progressively greater share of the available resources (Peet & Christensen, 1988). In such systems, small-stature forest herb specialists likely suffer from recruitment and persistence limitations in small and/or recent forest patches, due to increased light and mineral nutrient levels that primarily benefit a few generalist tall forbs, e.g. *Rubus fruticosus* agg. and *Urtica dioica*, or creeping woody species e.g. *Hedera helix* in our study. These species contribute to most of the aboveground biomass of the herb layer competing for light (Ma et al., 2018) and may thus competitively exclude smaller-statured forest specialists (Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999a; Verheyen & Hermy, 2016) and ultimately decrease herbaceous plant species richness relative to non-fragmented forests (Jacquemyn et al., 2001; Ma et al., 2018). This is especially the case along forest edges, which have been suggested efficient physical barriers against the arrival of forest specialists from neighboring patches (Fischer and Lindenmayer, 2007; Pickett et al., 2001).

Second, in highly-fragmented systems, forest patches are not sufficiently connected to allow most forest herbs to disperse among them, since forest herb species are well known for their low dispersal abilities (Vellend et al., 2007; Verheyen & Hermy, 2001a). Consistently, we found a tendency towards more forest specialist species accumulating locally as patch age increases (see the effect of covariates from the $\alpha_{FS} \sim \gamma_{FS}$ log-ratio models in Appendix 2-5), as predicted by the species-time relationship (Rosenzweig & Ziv, 1999) and previous observations in fragmented forests (Jamoneau et al., 2011). In other words, new forest patches are hardly

colonized by forest specialists, and it takes even much more time before they spread over the entire forest patch area. Forest specialists within new forest patches thus form scattered founding populations in an otherwise generalist-dominated plant community, so that the number of generalists increases faster than the number of forest specialists when increasing the sample area. The observed switch from linear to curvilinear-plateau AGR for forest specialists may thus be explained also in the absence of competitive exclusion (Lawton and Strong, 1981; Mouquet & Loreau, 2003), simply because only good colonizers from the surrounding area can quickly colonize a focal area. A similar pattern was reported for calcareous grasslands, where both the size of the species pool and community age influenced local species richness (Pärtel & Zobel, 1995). At the same time, populations of forest specialists in older patches may be hardly rescued by immigration and hence, be more exposed to stochastic extirpation (Hérault & Honnay, 2005; Jamoneau et al., 2012), a process potentially contributing to the reported decrease in the slope of the log-ratio model of forest specialists as fragmentation increases.

Forest fragmentation promotes generalist species

The fact that the number of generalist species co-occurring within forest plant communities tend to increase linearly with the number of generalist species available from a relatively larger area inside highly-fragmented systems is consistent with the idea that anthropogenic disturbances as well as edge effects (i.e. the part of a forest patch which is influenced by the surrounding landscape matrix) imposed by agricultural practices may create more favorable conditions for generalist species (Fischer & Lindenmayer, 2007b), at the expense of forest specialists.

Table 2-2: Outputs from the best candidate model *(see main text for the list of candidate models) for each of the two compiled datasets used to analyze the observed variation in the magnitude of the coefficient estimate or slope parameter of the log(γ) variable (i.e. the response variable) in the log-ratio model (see Equation 1 in the main text) of the* $\alpha \sim \gamma$ *relationship (AGR):* ***(1)*** $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ *(n = 90);* ***(2)*** $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ *(n = 180). Linear mixed-effects models (LMMs) were used to relate the response variable against fragmentation level (frag: NF, SF, HF), spatial scale (scale: 1, 2, 3, 4), species type (sp: FS vs. FG) and all possible two-way interactions between all three explanatory variables (see the materials and methods section in the main text). Bold values are representing significant (p < 0.05) effects. Grey cells show marginal and conditional R-squared values for each of the three best candidate models.*

(1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ **(n = 90)**			
	Coeff.	***t***	***p***
*Intercept*_NF	0.042	0.303	0.761
***frag*_HF**	**-0.447**	**-0.343**	**<0.001**
*frag*_SF	-0.102	-0.781	0.434
scale	0.029	0.56	0.575
R^2m/R^2c			0.129/0.129
(2) $\alpha_{FS/FG} \sim \gamma_{FS/FG}$ **[**$\alpha_{FS} \sim \gamma_{FS}$ **(n = 90) &** $\alpha_{FG} \sim \gamma_{FG}$ **(n = 90)] (n = 180)**			
	Coeff.	***t***	***P***
*Intercept*_NF&FS	-0.172	-1.001	0.306
***frag*_HF**	**-0.517**	**-2.176**	**0.029**
***frag*_SF**	**-0.689**	**-2.897**	**0.003**
*sp*_FG	-0.191	-0.802	0.422
frag_HF:sp_FG	**0.748**	**2.225**	**0.026**
frag_SF:sp_FG	**0.583**	**2.923**	**0.003**
R^2m/R^2c			0.173/0.173

Generalist plant species, that are usually fast-colonizers, have been shown to decrease in abundance from the edge to the forest interior, whilst the reverse pattern applied to slow colonizers such as ancient forest plant species (Hardiman et al., 2013). This niche partitioning

along edge-core gradients in forests can be explained by the well-known trade-off between survival in deep shade and growth in full light (Coomes, Kunstler, Canham, & Wright, 2009; Stephen P Hubbell & Foster, 1992), with the successful penetration of generalists into the forest interior usually limited by unfavorable light conditions (Harper et al., 2005; Hérault & Honnay, 2005). Edge effects have been reported to extend 20 to 50m (Hérault & Honnay, 2005; Murcia, 1995) and even 100 to 200m (Hardiman et al., 2013; Laurance et al., 2008) towards the forest interior. In our studied fragmented systems, this means that, to a certain extent, almost all forest patches are edge habitats rather than true forest interior habitats. Generalist species originating from the surrounding landscape are able to colonize edges of forest patches and subsequently migrate towards the patch interior, according to the so-called "biodiversity spillover effect" (Araujo Calçada et al., 2013b; L. A. Brudvig, Damschen, Tewksbury, Haddad, & Levey, 2009a). This spillover effect is likely more effective in highly-fragmented systems where forest patches are more exposed to lime and fertilizer leachates from adjacent croplands, compared to forest patches in the semi-fragmented systems. Moreover, the range of light conditions in nutrient-rich forests has been found to be greater than in nutrient-poor forests (Coomes et al., 2009), explaining why forests on fertile soils are more species-rich than their counterparts on nutrient-poor soils (Coomes et al., 2009; Cornwell & Grubb, 2003; Laanisto, Urbas, & Pärtel, 2008).

In contrast with fragmented systems, continuous forest patches in the non-fragmented system represent true forest interior habitats without edge effects, which offer light and soil conditions that are less suitable for generalist species. The shift from proportional sampling of generalists within highly fragmented systems towards community saturation within non-fragmented systems (Fig. 5c) can thus be explained by the absence of biodiversity spillover effect due to the absence of edge effects. We thus conclude that the shape of the AGR for generalists relates to the spatial distribution of generalist species within the forest patch rather

than to biotic interactions: regular over the entire patch, partitioned along the edge-core gradient and randomly clustered in highly-, semi- and non-fragmented systems, respectively.

2.7. Conclusion

Our results suggest that forest fragmentation affects the $\alpha \sim \gamma$ relationship by favoring generalist species over forest specialists (Karlson & Cornell, 2012; Myers & Harms, 2009). The striking different responses to forest fragmentation between forest specialists and generalists suggests that community assembly rules operate differently for these two guilds. In large and ancient forests, high quality habitat combined with the lack of fragmentation allows forest specialists to dominate the herb layer. Conversely, small and/or new forest patches isolated within a matrix of intensively cultivated landscapes are not only hardly colonized by dispersal-limited forest specialists, but also exposed to intense edge effects that allow generalist species to preempt space and resources and subsequently prevent forest specialists from establishment/persistence.

These findings have strong implications for biodiversity conservation and landscape planning, and fuel the single large or several small (SLOSS) debate (Diamond, 1975; D. Simberloff & Abele, 1982) by suggesting contrasting impact of forest fragmentation on the community assembly of forest specialists and generalists. Computing the $\alpha \sim \gamma$ relationship across a given landscape and separately between forest specialists and generalists will help to quickly visualize and assess the functioning state, and thus the quality, of forest metacommunities within the focal landscape. This may serve as a diagnostic tool to guide landscape management actions for biodiversity conservation, depending on whether one aims at maximizing the total number of species or at maximizing the conservation of patrimonial species such as forest specialists. At a regional scale, the "several small" strategy would indeed increase total species richness per forest patch (Fahrig, 2013a; Yaacobi, Ziv, & Rosenzweig, 2007), but at the expense of forest specialists by maximizing the proportion of generalist species, whilst the "single large" strategy would primarily benefit forest specialists, that are

also the most threatened species in a context of global environmental changes and management intensification of landscapes. Preserving the biggest, most ancient forest patches and maintaining/restoring connectivity between these patches should thus be encouraged in agricultural landscapes to ensure the long-term conservation of forest plant biodiversity, and its associated ecosystem services (Decocq et al., 2016).

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AUTHOR CONTRIBUTIONS

GD and JL conceived the study and the analytical framework; AJ collected the field data; AA TH, JL, CXGL and SW ran the statistical analyses; EGM conducted all GIS analyses. AA, JL and GD led the writing; all co-authors discussed the results, provided feedback and commented on the initial versions of the manuscript.

SUPPORTING INFORMATION

Appendix 2-1: Data table (raw data) used in the log-ratio model showing the species richness (forest specialists, generalists and total) as well as the value of several covariates at different spatial scales across the 116 studied forest patches.

Appendix 2-2: Species list.

Appendix 2-3: Description of the covariates used in the log-ratio models.

Appendix 2-4: Outputs from all candidate models (see main text for the list of candidate models) for each of the two compiled datasets used to analyze the observed variation in the magnitude of the coefficient estimates or slope parameter of the log(γ) variable (i.e. the response variable) in the log-ratio model (see Equation 1 in the main text) of the $\alpha \sim \gamma$ relationship (AGR): (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90); (2) $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ (n = 180). Linear mixed-effects models (LMMs) were used to relate the response variable against fragmentation level (frag: NF, SF, HF), spatial scale (scale: 1, 2, 3, 4), species type (sp: FS *vs*. FG) and all possible two-way interactions between all three explanatory variables (see the materials and methods section in the main text). Bold values are representing significant ($p < 0.05$) effects.

Appendix 2-5: Detailed outputs of two studied cases in the log-ratio models of $\alpha_{FS} \sim \gamma_{FS}$ (100 m^2 - 1000 m^2 and 1000 m^2 - Total patch scale) showing a significant effect of the covariate patch age.

Chapter 3: Winter cover crops decrease the abundance of weeds while increasing cash-crop yields

3.1. Résumé

Dans cette étude, nous visons à évaluer l'effet respectif et combiné de la réduction du travail du sol et des cultures de couverture d'hiver (i.e. semi direct sous couvert : SDSC) sur le recrutement d'espèces adventices des cultures et sur les rendements en tournesol (*Helianthus annuus*). En contrôlant la composition des espèces et la pression de propagules des espèces adventices, nous avons testé quatre traitements de rotation du couvert végétal : (i) *Camelina sativa* suivi d'une culture de tournesol, (ii) un mélange de *Fabacées et de Brassicacées* suivi par une culture de tournesol ; (iii) absence de couvert végétal hivernal suivi d'une culture de tournesol ; et enfin (iv) une modalité contrôle sur sol nue. Chacune des 4 modalités de rotation de couvert végétal a été testé en combinaison avec deux modalités de préparation du sol (travail du sol réduit vs. semis direct). L'ensemble des 6 modalités croisés a été répété en 3 blocs randomisés, soit 24 parcelles expérimentales (12 m × 8 m) au sein desquelles nous avons délimité 24 sous-parcelles (4m × 1m) afin d'éviter d'éventuels effets de bord. Dans chaque sous-parcelle, les graines de 40 espèces d'adventices des cultures ont été semées en mai 2017 et leur émergence a ensuite été surveillée à la mi-juillet, août et septembre 2017. La composition en espèces végétales spontanées (hors espèces présentes dans les semis) a également été inventoriée au début juillet 2017 et avant l'émergence des espèces adventices semées pour établir une situation initiale de référence. Nous avons utilisé des modèles linéaires généralisés pour analyser l'effet de la rotation du couvert végétal et de la préparation du sol sur la richesse en espèces adventices semées, l'abondance (nombre d'individus) de chaque espèce adventice semée et le rendement en tournesol. Nous avons également utilisé des modèles linéaires à effets mixtes pour analyser les changements d'abondance relative des espèces par rapport à la situation de référence avant émergence des espèces adventices semées. Nos résultats montrent que le travail réduit du sol

peut augmenter la richesse en espèces adventices dans certaines circonstances, ainsi que l'abondance de deux espèces annuelles (*Viola arvensis et Fumaria officinalis*). Le mélange Fabacées-Brassicacées d'hiver réduit l'abondance des espèces adventices les plus dominantes (e.g. *Echinochloa crus-galli*) tout en augmentant le poids moyen des graines de tournesol par tige. Indépendamment du traitement du sol, nous avons constaté que *Camelina sativa* favorise la présence d'espèces adventices patrimoniales aux dépens des espèces nuisibles. Nous concluons que les semis directs associés au mélange Fabacées-Brassicaceés d'hiver permettent de contrôler l'abondance des espèces adventices tout en augmentant le rendement des cultures commerciales, et répondent donc aux critères d'une agriculture durable.

Mots clés : *pratiques agricoles, communauté de mauvaises herbes, travail du sol réduit, couverture végétale permanente, Camelina sativa.*

3.2. Article title

Winter cover crops decrease the abundance of weeds while increasing cash-crop yields

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ABSTRACT

In this study, we aim to evaluate the respective and combined effect of soil tillage reduction and winter cover crops (CCs) on both weed species recruitment and sunflower (*Helianthus annuus*) yields. By controlling the species composition and propagule pressure of weeds, we tested four soil cover rotation treatments with winter CCs (either *Camelina sativa* or a winter CC-mix of Leguminosae-Brassicaceae) or nothing (control) followed by a sunflower culture or nothing (control) in combination with two soil preparation treatments (reduced tillage *vs*. direct seedling) in a randomized complete block design with three replicates per treatment. Our experimental field thus comprises 24 subplots (4m × 1m) embedded in the interior of 24 experimental plots (12m × 8m) to avoid possible edge effects. In each subplot, seeds of 40 weed species were sown in May 2017 and seedling emergence was subsequently monitored in mid-July, August and September 2017. The vegetation was also surveyed in early July 2017 to estimate baseline conditions. We used generalized linear models to analyze the effect of soil cover rotation and soil preparation on species richness, abundance (i.e. number of individuals), and sunflower yield. We additionally used linear mixed-effects models to analyze species relative abundance changes with respect to the baseline survey. Our results show that reduced tillage may increase weed species richness under some circumstances, as well as the abundance of two annual species (i.e. *Viola arvensis* and *Fumaria officinalis*). Winter CC-mix reduces the abundance of the most dominant weed species (i.e. the exotic grass *Echinochloa crus-galli*) while increasing the average weight of sunflower seeds per stem. Irrespective of the tillage treatment, we found that *C. sativa* favors the presence of patrimonial weed species at the expense of noxious species. We conclude that direct seedling associated with winter CC-mix allows controlling weed abundance while increasing cash-crop yields, and thus meets criteria for a sustainable agriculture.

KEYWORDS

Agricultural practices, weed community, reduced tillage, permanent plant cover, Camelina sativa.

RUNNING HEADLINE

Impact of different agricultural practices on weed community

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ARTICLE TYPE

Research article

3.3. Introduction

A considerable increase in food production has been achieved since WWII by using monocultures of high-yielding crop varieties, huge amount of fertilizers and pesticides, and increased consumption of fossil fuel, water and topsoil (David Tilman, 1999b). Agriculture intensification, however, led to unprecedented rates of environmental degradation, including soil, air and water pollution, soil erosion, and biodiversity loss (Galloway et al., 2008; R. A. Robinson & Sutherland, 2002; Stoate et al., 2001). In particular, arable plant species (weeds) dramatically declined in many rural landscapes over the last few decades (Firbank, 2008; Rich & Woodruff, 1996; Storkey et al., 2013; Sutcliffe & Kay, 2000). Weeds not only represent an important part of plant biodiversity in otherwise highly artificialized farmlands, but also have cultural and aesthetic values (Swift, Izac, & van Noordwijk, 2004). They also deliver important ecosystem services, by serving as forage for pollinators, food for granivorous rodents, birds and insects, as well as shelter for auxiliary arthropods (Isaacs, Tuell, Fiedler, Gardiner, & Landis, 2009; Marshall et al., 2003).

Making agriculture more sustainable and reducing its negative impacts on ecosystem integrity and human health, while maintaining or increasing yields, is thus challenging for the 21st century (Fedoroff et al., 2010). This is the rationale behind conservation agriculture, a system of agronomic practices that include tillage reduction, permanent soil cover, and crop rotations (Hobbs, 2007; Nichols et al., 2015; Palm et al., 2014). However, reduced tillage is hardly adopted by farmers since it is believed to increase weed infestation, which in turn can be responsible for decreased crop yields (Belz, 2007; Einhellig, 1996). Empirical evidence for this statement is inconstant and crop-specific (Armengot et al., 2015; Légère et al., 2013) and it is likely that a threshold in weed abundance must be passed before effective yield declines (Armengot et al., 2015; Sans et al., 2011). Most weeds are annual species which are adapted to cyclic soil disturbances and cropping (Gaba et al., 2017), and hence are r-strategists (J. Philip

Grime, 2006b) with a short life cycle, high fecundity and fertility, and dense soil seed banks (Bakker, Poschlod, Strykstra, Bekker, & Thompson, 1996; J. P. Grime, 1998). The seed bank is the main source of weed occurrence in crops (Cavers & Benoit, 1989) and inversion tillage system is considered to reduce both seed bank density and recruitment from the seed bank (Nichols et al., 2015).

There is thus a balanced trade-off to be found between the preservation of weed diversity and maintenance of crop yields. The use of cover crops (CCs) has been suggested an efficient mean of suppressing weed emergence in reduced till systems (Baraibar, Hunter, Schipanski, Hamilton, & Mortensen, 2018; Kunz, Sturm, Varnholt, Walker, & Gerhards, 2016; Rueda-Ayala, Jaeck, & Gerhards, 2015; Teasdale, Coffman, & Mangum, 2007), through direct competition for space and resources or the release of allelochemicals (Björkman et al., 2015; Finney, Eckert, & Kaye, 2015). The suppression of certain competitively dominant weed species might release other weed species from competitive exclusion, thereby increasing weed species diversity while increasing yields of the cash crop (D. R. Clements, Weise, & Swanton, 1994; Radicetti, Mancinelli, & Campiglia, 2013), but this hypothesis has not been tested so far.

The common practice is to use winter CC between two cash crops, with residues retained on the ground (Mirsky, Curran, Mortenseny, Ryany, & Shumway, 2011; Teasdale & Mirsky, 2015). It has been suggested that a mixture of CC species (e.g. grasses and Leguminosae) is more weed suppressive than a monoculture (Baraibar et al., 2018; Lawson, Cogger, Bary, & Fortuna, 2015) due to functional complementarity (Hooper et al., 2005; Loreau et al., 2001b) and thus greater CC biomass (Baraibar et al., 2018; Lawson et al., 2015). However, empirical support is still limited and CC impacts on weed communities likely depend upon CC types, sowing and mulching dates, and cash crop type (Alonso-Ayuso, Escudero, Guignard, & Weintraub, 2018; Buchanan, Kolb, & Hooks, 2016; Campiglia, Radicetti, & Mancinelli, 2012). An overlooked alternative is the insertion of a spring or summer short-cycle cash crop between

two main crops, allowing the harvest of three cash crops over two years. Several candidate species can be found in the *Brassicaceae* family, which can be cultivated as oil seed plants and are also well documented for their allelopathic effects on weed germination (Haramoto & Gallandt, 2005; Petersen, Belz, Walker, & Hurle, 2001). However, their efficacy in controlling weeds has been poorly documented so far. Here we aim at contributing to fill this gap of knowledge.

Assessing the impact of cropping systems on weed community diversity is not a trivial task. Available studies usually used an experimental design where cash and CCs were controlled in a randomized complete block design (Alonso-Ayuso et al., 2018; Baraibar et al., 2018) but without controlling for local and proximal weed species pools. Such study designs assume that the distribution of weed species is more or less homogeneous both aboveground (i.e. standing individuals and seed rain) and belowground (i.e. soil seed bank). This is obviously an unrealistic assumption, especially in reduced tillage systems. Seeds exhibit highly clustered spatial patterns, both as seed rain and belowground (Dessaint, Chadoeuf, & Barralis, 1991; Plue & Hermy, 2012), due to the already patchy distribution of mother plants, itself associated with the spatial heterogeneity of the environment (Plue & Hermy, 2012). Consequently, the fundamental assumption of the independence of observations underlying most statistical analyses is likely violated. Spatial autocorrelation at the plot scale must thus be compensated for (Fortin, Drapeau, & Legendre, 1990) or, alternatively, should be overcome by using an adequate study design. Here, we retained the latter option, by controlling for the seed input (i.e. species composition and number of seeds per species).

The objective of this study is to evaluate the respective and combined effect of soil preparation (reduced tillage *vs*. direct seedling) and CCs (two different CC *vs*. no CC) on weed species recruitment and yields in following sunflower cultures. For this purpose, we implemented a controlled field experiment using a randomized block design, with barley-

sunflower-wheat as principal cash crop rotation and either a functionally diverse mixture – including Leguminosae and Brassicaceae – or a *Camelina sativa* harvested cash crop as winter CC inserted between barley and sunflower. Here, we assume that direct seedling of winter CC, either throughout the diversity-complementarity hypothesis or via the allopathic effect of *C. sativa*, is likely to suppress the most dominant and competitive weed species while increasing weed species richness and sunflower yields.

3.4. Materials and Methods

3.4.1. Study site and experimental design

We conducted our experiment in an arable field located in North France (Sorrus; latitude: 50.463208°; longitude: 1.748206°; altitude 40m) (Fig. 1A). The climate is oceanic, characterized by a mean annual precipitation of 872mm and a mean annual temperature of 10.8°C. Monthly precipitation are regularly distributed throughout the year and mean temperature ranges from 4.7°C (January) to 17.6°C (August). The experiment was installed on plateau position with Luvisol developed on loess, a silt dominated material with a high proportion of sand. The regional landscape is dominated by croplands, intensively cultivated for cereals, rapeseed and sugar beet. Prior to the experiment, the field was cultivated with direct seedling farming practices since 15 years.

We used a randomized complete block design (Figs. 1B and 1C) with three blocks (3 repetitions), and two factor variables with two and four levels of treatments, respectively, hence making 8 different combinations of treatments repeated 3 times (N = 24 plots of 12m × 8 m):

(i) Soil preparation treatments (2 levels): "reduced tillage" with a non-inversion method (using a Chisel plough) *vs*. "no tillage", also refereed as "direct seedling";

(ii) Soil cover rotation treatments (4 levels): the first scenario was *Camelina* (*Camelina sativa*) in intercropping followed by sunflower (*Helianthus annuus*) to test the potential allelopathic effect of *Camelina* on weed recruitment. The second scenario was an intercropping with a functionally diverse and complementary mixture of CCs (*Raphanus sativus, Fagopyrum esculentum*, *Trifolium michelianum*, *T. pratense* and *T. hybridum*) followed by sunflower to test the diversity-complementarity hypothesis on weed recruitment. The third scenario was nothing during winter followed by sunflower, which is the conventional rotation; and the fourth scenario was nothing all the time, i.e. the control treatment.

3.4.2. Site preparation

Chisel plowing was applied on 21st July 2016, just after the previous barley crop was harvested, across 12 out of the 24 experimental plots. On the same day, the winter CC was sown (i.e. CC-mix and *Camelina*) in half of the studied plots (see Fig. 1C for details on plot location across the experimental site). Nitrogen fertilizer (ammonium nitrate NH_4NO_3) was applied at a rate of 80 $kg.ha^{-1}$ to all the plots through the fertilizer hopper on 8 August 2016. In the first two weeks of April 2017, deep ripping and power harrowing were performed for the plots with reduced tillage treatment. On the same day, glyphosate (Round-up®) and anti-slug treatments were applied over the 24 plots. On 28 April 2017, sunflower (cash-crop) was sown in its corresponding plots and, on the next day, herbicide (Prowl400®) was applied over the 24 plots. On 14 June 2017, another round of nitrogen fertilizer (ammonium nitrate NH_4NO_3) was applied at a rate of 70-80 $kg.ha^{-1}$ to all the plots. All details concerning the planning of events to ensure site preparation are presented in the timeline in Appendix 3-1.

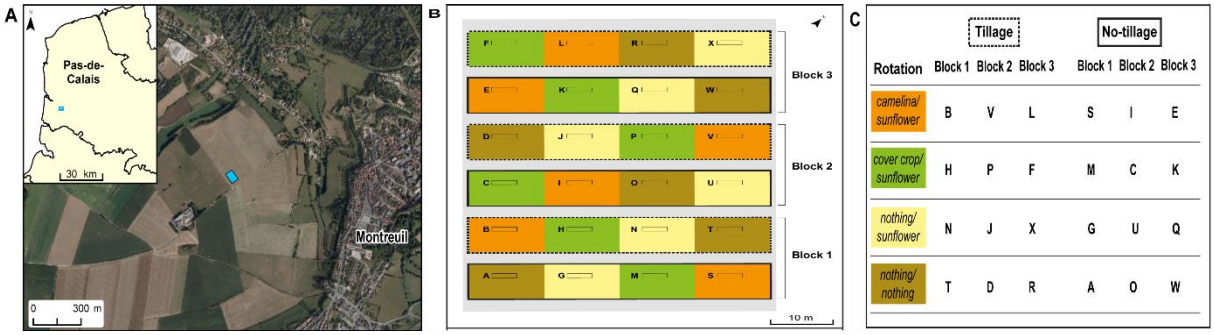

***Figure 3-1: Experimental site (A)**, where the field was organized in a randomized block design **(B)** with 3 repetitions for every treatment **(C)** in studying the effect of two different soil preparations (reduced tillage vs direct seedling) and four different soil cover rotations on weed community.*

3.4.3. Seed preparation

We had chosen 40 weed species (Appendix 3-2) to cover a large spectrum of life forms (grass *vs*. forbs) and plant traits such as life span (annuals *vs*. perennials), canopy height and dispersal

strategy (e.g. gravity-, wind-, bird-, ant-dispersed). Seeds were collected from wild plants growing in regional cultivated lands to ensure a local provenance, except for three species (*Cyanus segetum, Coriandrum sativum,* and *Reseda lutea*) for which we used commercial seeds. The total number of seeds available for each of the 40 species was divided into 27 equal portions (24 portions for the experimental site and 3 portions for greenhouse germination tests) (see Appendix 3-2 for more details on propagule pressure). Then, we pooled each portion of the 40 species into a single mixture to get one mixture for each of the 27 experimental units. By doing so, we ensured a similar composition and propagule pressure across the experimental sites and for the germination test. On 18 May 2017, the seed mixture was sown in each of 24 subplots (1m × 4m) that were disposed inside each 12m × 8 m experimental plots to avoid edge effects (Fig. 1B), and every subplot was protected with a porous net during one month to avoid seed predation by birds and small rodents. The next day, we settled the greenhouse experiment in triplicate (3 mixtures of seeds) using the same seed mixture. Seeds were spread over steam-sterilized compost-filled containers and allowed to germinate under a natural light regime and a temperature regime ranging from 25/20 °C day/night. The containers were kept moist by regular watering. Three control containers containing only steam-sterilized compost were distributed among the other containers to detect eventual contamination. No contamination was detected. We monitored seedling emergence to determine seed viability. All seedlings were identified, counted and removed at weekly intervals from May 2017 until June 2018.

3.4.4. Vegetation survey and data collection

On 4 July 2017, we performed a baseline vegetation survey across all 24 plots to record the percentage cover of each vascular plant species occurring at the beginning of the experiment. This allowed us to estimate the local weed species pool available before seed germination started. Then, we re-surveyed each subplot at 3 dates throughout the vegetation season (17 July, 29 August, 26 September): we counted the total number of individuals per species. For highly

abundant species (i.e. *Echinochloa crus-galli*, *Poa annua*, *Senecio vulgaris* and *Viola arvensis*), we randomly put a 14.5cm × 23cm wooden frame on the ground and counted the total number of individuals occurring within that frame before multiplying it by the total number of frames we could arrange to estimate the area covered by the species across the subplot.

On 26 September 2017, following the last vegetation resurvey, we randomly collected 10 sunflower individuals from an area of $1m^2$ within each of the 24 studied subplots (240 individuals in total). Each of the 240 harvested individuals was measured for plant canopy height prior to harvest. Back from the field, sunflower seeds were separated from their corresponding stem before being weighted and counted separately for each of the 240 individuals.

3.4.5. Data analysis

Based on our full factorial experimental design, we tested the respective pure effects of soil preparation (reduced tillage vs. direct seedling) and soil cover rotation (Camelina / sunflower, CC-mix / sunflower, nothing / sunflower, nothing / nothing) as well as the two-way interaction effect between both variables on: (1) weed species richness; (2) weed abundance (total abundance and relative abundance per species); and (3) sunflower yield. In addition to testing the effects of soil preparation and soil cover rotation on the absolute value of weed abundance (i.e. both the overall abundance across all weed species and the species-specific abundance), we also analyzed changes in the relative abundance of weed species over time to test which weed species is going up or down in the ranking of abundance values across the different conditions.

3.4.5.1. Species richness

Here, the response variable is species richness per subplot (count data: one richness value per subplot). Hence, we used the "glm" function from the "stats" package to fit generalized linear

models (GLMs) with a Poisson distribution. We built a list of candidate models including, as predictor variables, soil preparation or soil cover rotation or both simultaneously (see Appendix 3-3 for the full list). In addition to these two variables of main interest for the study, some of the candidate models included "block" (B1, B2, B3) and "date" (17th July, 29th August, 26th September) as covariates to account for potential confounding effects. All possible two-way interaction terms involving soil preparation or soil cover rotation were tested. For each candidate model, we computed the Akaike Information Criterion (AIC) and ranked all models according to their AIC values, with the best model being the one with the lowest AIC value (Burnham & Anderson, 2002). Once the best candidate model was selected, we extracted the coefficient estimates, standard errors and associated p-values for each of the predictor variables listed in the best model. Finally, we ran an Analysis of Variance (ANOVA) of the best model, using Type-II or Type-III ANOVA depending on whether there was a non-significant or a significant interaction term, respectively. We used the "ANOVA" function from the "car" package in R.

3.4.5.2. Species abundance

Here, the response variable is multivariate with the individual species abundance by subplot matrix being the matrix of response variables (zero-inflated distribution: several species abundance values, including many zeros, per subplot). Hence, we used a modelling approach very similar to the GLM approach with a negative binomial distribution but adapted to high-dimensional data, such as multivariate abundance data in ecology (cf. the species × subplot matrix of abundance values) (Y. Wang, Naumann, Wright, & Warton, 2012). Similar to our analyses on species richness, we tested the same list of candidate models (Appendix 3-3) using the same model selection procedure as above but running the "manyglm" function from the "mvabund" package in R (Y. Wang et al., 2012). Once the best candidate model was selected, we extracted the global statistics across all species as well as species-specific statistics such as

the coefficient estimates of all the species individually to study their corresponding behavior according to the predictor variables listed in the best model. We used the "anova.manyglm" function from the "mvabund" package to generate an analysis of deviance table for the best candidate model.

3.4.5.3. Changes in species' relative abundance

For each vegetation survey (late July, August, September), including the baseline survey (early July), we ranked weed species according to their abundance values. In case of absence of one or several of the species in any of the subplots and at any dates, we ranked these species after the least abundant species. Then, we computed for each species separately, the differences in their rank value between a given vegetation survey and the baseline survey, leading to three rank difference values per species and per subplot. Using each of these values as the response variable, we ran linear mixed-effects models (LMMs) with a Poisson distribution (similar to count data). We used soil preparation, soil cover rotation and block as the three fixed effect variables in the model and set species as a random variable interacting with both soil preparation and soil cover rotation (random slope terms) in the model. Because the three rank differences per species and per subplot are not independent from each other (same baseline conditions each time), we ran our single candidate model three times. Finally, we extracted, for each species, the estimated mean and 95% confidence interval of the rank difference.

3.4.5.4. Crop yield

Crop yield was quantified by measuring both sunflower height and the average weight of seeds per stem. Both sunflower height and weight of seeds per stem were treated as response variables in GLMs with a Gaussian distribution. We tested the same list of candidate models (Appendix 3-3) and used the same approach for model selection as we did for analyzing species richness and species absolute abundance.

All statistical analysis were performed using the “car”, “ggplot2”, “gridExtra”, “lme4”, “Matrix”, “MuMIn”, “mvabund” , “nlme”, “reshape2” and “stats” packages in the R software environment version 3.4.1 (R Core Team 2017).

3.5. Results

A total of 40 weed species were monitored in both field and greenhouse over the study period. Twenty-eight species germinated in the greenhouse while 35 species germinated in the field (see Appendix 3-4 for details on species germination success) regardless of both the soil preparation and soil cover rotation. The majority of these species were characterized by autumn germination and early spring flowering. Poa annua & Echinochloa crus-galli were the most abundant species across all treatments studied (see Appendix 3-5 for detailed information about species richness and species total abundance). These species (Poa annua & Echinochloa crus-galli) were highly abundant in the field, likely due to their presence and persistence in the soil seed bank.

3.5.1. Species richness

The best candidate model to explain weed species richness includes soil cover rotation, date, and the interaction between block and soil preparation (see M24 in Appendix 3-3 for the complete model formula). We found a significant interaction effect between block and soil preparation on weed species richness (Table 1 and Table 2), such that reduced tillage had a negative impact on weed species richness in block 3 but a positive impact in blocks 1 and 2 (Table 1). We found no effect of soil cover rotation on weed species richness.

Table 3-1: Coefficient estimates from the best candidate model *(see M24 in Appendix 3-3) linking species richness to soil preparation, soil cover rotation, date and block effect. Bold values represent significant (p<0.05) effects. The intercept represents the average weed species richness value for block1 in July under direct seedling treatment and under the Camelina / sunflower rotation treatment. Estimates need to be interpreted against the intercept value. Hence, the average weed species richness value for block1 in July under reduced tillage treatment and under the Camelina / sunflower rotation treatment is 1.403+0.631 = 2.034.*

Effect	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.403	0.194	6.003	**<0.001**
block2	-0.048	0.220	-0.22	0.825
block3	0.579	0.192	3.008	**0.002**
reduced tillage	0.631	0.190	3.308	**<0.001**
CC-mix /sunflower	0.020	0.142	0.142	0.886
nothing/nothing	0.060	0.141	0.424	0.671
nothing/sunflower	-0.218	0.152	-1.43	0.151
August	-0.237	0.126	-1.87	0.060
September	0.093	0.130	0.717	0.473
block2: reduced tillage	-0.030	0.274	-0.11	0.912
block3: reduced tillage	-0.729	0.253	-2.87	**0.004**

Table 3-2: Output of Type III ANOVA representing the best candidate model *(M24 in Appendix 3-3) studying species richness with the change of soil preparation, soil cover rotation, date and block. Bold values represent significant (p<0.05) effects.*

	Sum Sq	Df	F value	p value
(Intercept)	471	1	122,5	**<0,001**
rotation	21	3	1,79	0,1595
reduced tillage	55	1	14,33	**<0,001**
block	20	2	2,61	0,0814
date	19	2	2,50	0,0909
reduced tillage:block	49	2	6,41	**0,0029**

3.5.2. Species abundance

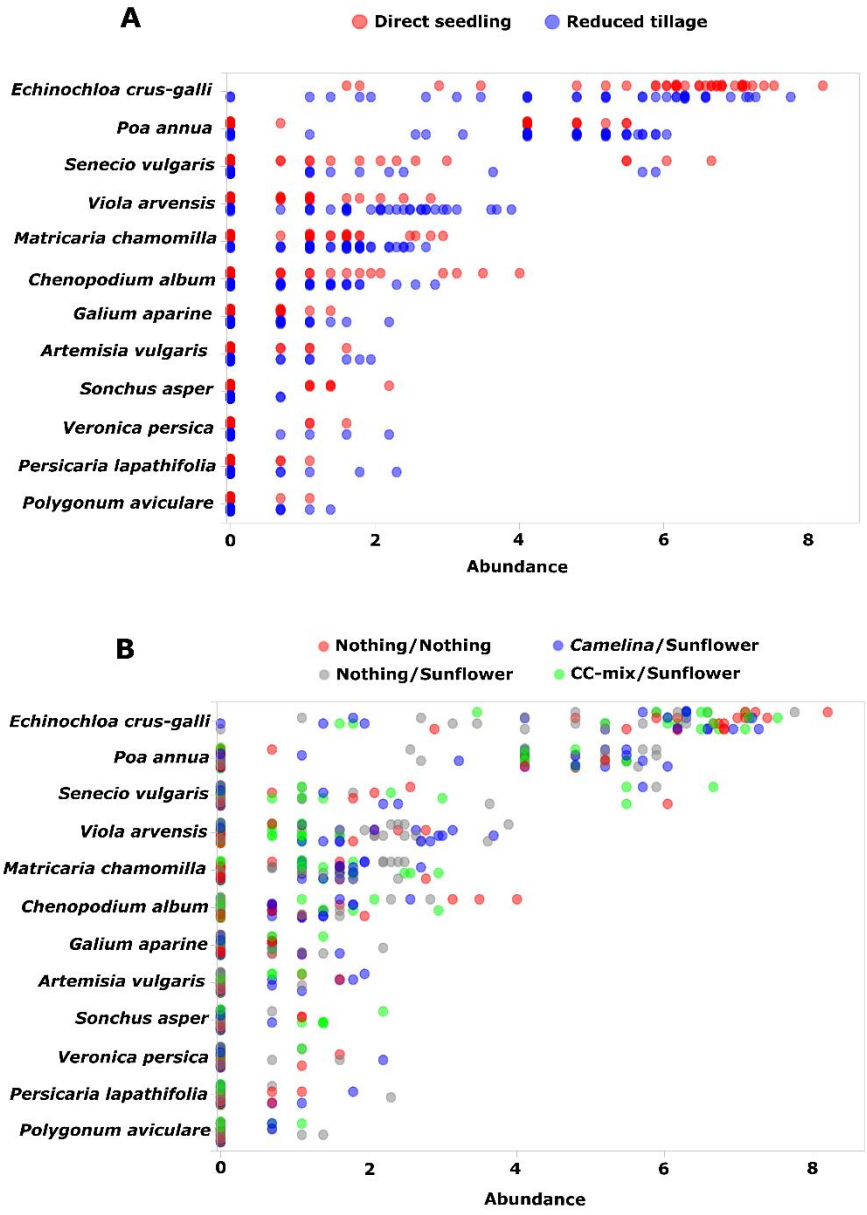

Figure 3-2: Abundance of weed species *according to* ***(A):*** *the difference in soil preparation (reduced tillage vs. direct seedling treatments) and* ***(B):*** *the different soil cover rotation (4 levels). Only the most abundant species are presented.*

Similarly to the analyses on species richness, the best candidate model to explain the overall abundance (number of individuals) of weed within the subplots includes soil cover rotation, date, and the interaction between block and soil preparation (see candidate model M24 in Appendix 3-3 for the complete model formula). Yet, the interaction term between block and

soil preparation was not significant this time. We found that the overall abundance of weed, irrespectively of the species considered, was higher (Table 3): during July than during August; when there was no soil cover rotation (nothing / nothing) than when Camelina was used in intercropping followed by sunflower; under reduced tillage than under direct seedling; and in block 3 than in block 1 (see Appendix 3-6.A and F.B for the effect of both block and date respectively on the most abundant weed species). In addition, further analyses at the species level (Table 4) showed that the abundance of some weed species are clearly affected by both soil cover rotation and soil preparation (see Appendix 3-7 for more details about all the studied species). For instance, the abundance of both Viola arvensis and Fumaria officinalis increased under reduced tillage (Fig. 2A and Table 4 respectively) while the abundance of the most dominant weed species, i.e. Echinochloa crus-galli, decreased when using a CC-mix in intercropping followed by sunflower (Table 4).

Table 3-3: Overall statistics of the best candidate model selected *(see M24 in Appendix 3-3 for the model formula) to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance (outcomes of the "manyglm" function from the "mvabund" package). Bold values represent significant ($p<0.05$) effects across all 40 studied weed species. Coefficient estimates are available at the species level (see Table 4 and Appendix 3-7).*

Effect	wald value	Pr(>wald)
(Intercept)	20.56	**<0.001**
block2	3.405	0.212
block3	5.745	**0.005**
reduced tillage	5.824	**0.008**
CC-mix /sunflower	5.976	**0.02**
nothing/nothing	7.052	**<0.001**
nothing/sunflower	4.522	0.103
July	8.934	**<0.001**
September	5.024	**0.047**
block2:reduced tillage	2.538	0.551
block3:tillage	2.792	0.501

Table 3-4: Detailed statistics of the best candidate model selected *(see M24 in Appendix 3-3 for the model formula) at the species level to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance individually. Bold values represent significant (p<0.05) effects* ***(A)*** *and their corresponding coefficient* ***(B)*** *across the five affected weed species (see Appendix 3-7 for the complete species abundance analysis).*

A) P-Table	***Echinochloa crus-galli***	***Fumaria officinalis***	***Senecio vulgaris***	***Veronica persica***	***Viola arvensis***
block	0,078	0,986	0,986	0,974	0,953
reduced tillage	0,251	**0,04**	0,988	0,966	**0,001**
rotation	**0,038**	1	0,084	1	1
date	0,484	0,16	**0,001**	**0,012**	0,911
block:reduced tillage	0,943	0,997	0,974	0,417	0,343
B) Coefficient Table	***Echinochloa crus-galli***	***Fumaria officinalis***	***Senecio vulgaris***	***Veronica persica***	***Viola arvensis***
(Intercept)	7,63	-13,61	-5,58	-24,95	-0,12
block2	-0,43	0	-0,33	0	0,13
block3	-1,48	0	1,09	12,61	2,03
reduced tillage	-1,02	**12,1**	-0,94	9,34	**2,19**
CC-mix /sunflower	**-1,05**	-0,41	1,09	2,2	0,44
nothing/nothing	**0,62**	-0,41	3,71	0,38	-0,46
nothing/sunflower	**0,03**	-0,41	2,48	-0,59	-0,16
July	-0,75	2,08	**7,4**	0	-0,87
September	-0,5	-9,21	**1,32**	**13**	-0,67
block2:reduced tillage	0,64	-1,79	-0,68	1,97	0,92
block3:reduced tillage	-0,23	-1,1	-0,77	-10,86	-1,37

3.5.3. Changes in species' relative abundance (species rank difference)

Irrespective of soil preparation (reduced tillage *vs*. direct seedling), using *Camelina* as a winter CC before sunflower had important effects on the ranking of weed species abundance over time relative to the control and conventional treatments which had no effect (Fig. 3). For instance, some perennial species in particular (*Artemisia vulgaris, Plantago lanceolata*) were clearly positively impacted by *Camelina* at all dates, as well as several annual species (e.g. *Coriandrum sativum, Centaurea cyanus, Poa annua, Matricaria chamomilla*) in July and August. At the same time, *Camelina* had a negative impact on the relative abundance of the geophyte *Cirsium arvense*, as well as of several annuals (e.g. *Persicaria maculosa, Chenopodium album, Senecio vulgaris, Capsella bursa-pastoris, Atriplex patula*). Noteworthy, *Cyanus segetum* and

Coriandrum sativum are patrimonial species while *Cirsium arvense* is a noxious weed. Using CC-mix as winter cover before sunflower only had a marginal effect on the ranking of weed species abundance during July favouring the relative abundance of some species like *Artemisia vulgaris*, *Coriandrum sativum*, and *Centaurea cyanus* under direct seedling treatment but decreasing the relative abundance of the same species under reduced tillage treatment (see Fig. 3). The opposite was true for *Perisicaria maculosa* (see Appendix 3-8 for relative abundance of the studied weed species).

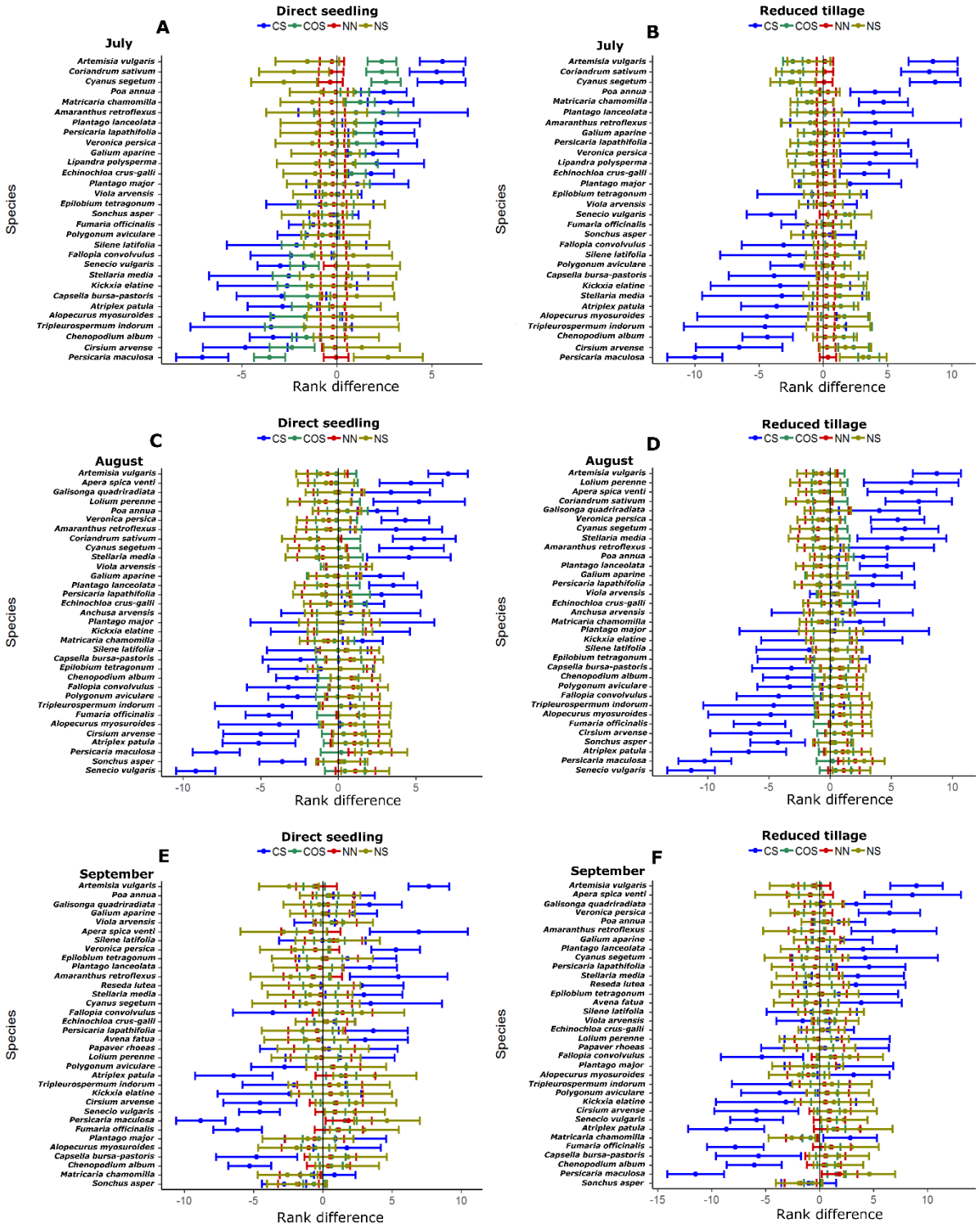

Figure 3-3: Estimated mean and 95% confidence interval of the rank difference values *from the model used (see section 2.5.3 in materials and methods) at 3 different dates (July - August - September) studying the relative abundance change of weed species as function of soil cover rotations (4 levels) and soil preparation (reduced tillage vs direct seedling). CS corresponds to Camelina and sunflower rotation. COS corresponds to CC-mix with sunflower rotation. NN*

corresponds to the soil left without both winter and summer covers. NS corresponds to soil left in winter and cultivated with sunflower as summer crop. Species are oriented along the vertical axis according to decreasing order of the mean rank difference between treatments. Note that only the species that succeeded to germinate in either the subplots or the plots (baseline study) are presented along the vertical axis.

3.5.4. Crop yield

The best candidate model to explain sunflower height (Appendix 3-9.A) and the average weight of seeds per stem (Appendix 3-9.B) includes block, soil cover rotation, and soil preparation as predictor variables (see candidate model M13 in Appendix 3-3 for the complete model formula). None of the variables were significant in explaining sunflower height but the average weight of seeds per stem was significantly higher in block 3 than in block 1 and when CC-mix were used in intercropping (Table 5).

Table 3-5: Coefficient estimates from the best candidate model *(see candidate model M13 in Appendix 3-3) linking crop yield, either measured as sunflower height* ***(A)*** *or as the average weight of sunflower seeds per stem* ***(B)****, to soil preparation, soil cover rotation (only 3 levels here as the nothing / nothing control treatment could not be considered for crop yield) and block effect. Bold values represent significant (p<0.05) effects. The intercept represents the average crop yield value (height in cm or weight in g) for block1 under the Camelina / sunflower rotation treatment. Estimates need to be interpreted against the intercept value. Hence, the average sunflower seed mass per stem for block3 under the CC-mix / sunflower rotation treatment is 34.7+42.1+21.9 = 98.7 g.*

	(A) Sunflower height			
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	146	8.92	16.3	**<0.001**
block2	-3.83	8.92	-0.42	0.675
block3	7.66	8.92	0.85	0.407
CC-mix /sunflower	-0.66	8.92	-0.07	0.941
nothing/sunflower	1.99	8.92	0.22	0.826
reduced tillage	12.6	7.28	1.73	0.107
	(B) Weight of seeds per stem			
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	34.7	9.69	3.58	**<0.001**
block2	9.89	9.69	1.02	0.327
block3	42.1	9.69	4.34	**<0.001**
CC-mix /sunflower	21.9	9.69	2.26	**0.042**
nothing/sunflower	5.08	9.69	0.52	0.609
reduced tillage	9.46	7.91	1.19	0.254

3.6. Discussion

In this study, we test the relative importance of soil preparation and winter CCs in explaining weed community dynamics over a single season (i.e. richness, abundance, and change in relative abundance). We evidence that winter CC suppresses the most dominant weed species (e.g. *Echinochloa crus-galli*), especially when using a Leguminosae-Brassicaceae mixture as CC. Winter CC does not impact weed species richness, while soil preparation (i.e. reduced tillage *vs*. direct seedling) has complex effects. Interestingly, the use of winter CC-mix was associated with increased cash-crop yield, in contrast with *Camelina*. Below, we discuss these main results in details.

3.6.1. Impact of soil preparation

Soil preparation, not CCs, impacts weed species richness with reduced tillage interacting with experimental block to increase species richness in two of the three blocks, as compared to direct seedling treatment, while the reverse was found in the third block. The effect of soil preparation on weed species richness is still debated. Reduced tillage has been shown to increase the number of weed species (M. I. Santín-Montanyá, Martín-Lammerding, Zambrana, & Tenorio, 2016), but this effect likely depends upon crop rotation (Legere, Stevenson, & Benoit, 2005; Stevenson et al., 1998). Compared to conventional tillage (i.e. inversion tillage; Clements et al., 1994) and direct seedling (Kraska, 2012; Plaza, Navarrete, & González-Andújar, 2015), reduced tillage appeared less detrimental to weed species diversity, by providing safe sites for weed establishment. However, in contrast with our findings, other studies have found no increase in weed species richness in reduced tillage systems when compared to other soil preparation treatments (i.e. direct seedling and conventional tillage; Barroso et al., 2015; Bilalis et al., 2001). The 3-years study of Barroso et al., (2015) assessed the effect of two different cropping systems (*Medicago sativa* & *Triticum aestivum*) under three different soil preparations (herbicide, tillage and reduced tillage) and showed no significant impact of soil preparation on

both weed species diversity and abundance. Mas and Verdú, (2003) showed that during a 4-years study of three different crops (*Pisum sativum, Triticum aestivum* & *Hordeum vulgare*); direct seedling system recorded the highest weed diversity as compared with other tillage systems (i.e. conventional tillage). Noteworthy, the previously mentioned studies (Barroso et al., 2015 & Mas and Verdú, 2003) are considered long-term studies unlike our study which was a short-term assessment (single season), inferring the importance of the study duration in explaining the significant effect of soil preparation on weed community assembly. It has been argued however, that there is no clear increase or decrease of weed diversity with the change of tillage practices alone (Barroso et al., 2015). This suggests that the interaction between tillage treatment and crop rotation from one side (Legere et al., 2005; Swanton, Clements, & Derksen, 1993), and between tillage treatment with herbicide use from the other side (Locke & Bryson, 1997; Charles L. Mohler, 1993), might be crucial to weed community structure. In our study, the block effect cannot be attributed to differences in interspecific competition among blocks (J. P. Grime, 1998; Huston, 1979) since the dominant grass species (*Echinochloa crus-galli*) as well as the overall abundance of all weed species is the lowest in the block where species richness is lower, irrespective of the soil treatment. Instead, the block effect may be attributed to small-scale differences in unmeasured local environmental conditions, such as soil fertility (Stevenson et al., 1997) or other abiotic factors, which can have an overriding effect on soil preparation in explaining weed species richness (Pal et al., 2013).

While reduced tillage increases the relative abundance of some annual species (e.g. *Fumaria officinalis* and *Viola arvensis*), direct seedling rather promotes perennial species (e.g. *Artemisia vulgaris*). This is highly consistent with former findings (María Inés Santín-Montanyá, Zambrana-Quesada, & Tenorio-Pasamón, 2018; A. G. Thomas & Frick, 1993; Travlos, Cheimona, Roussis, & Bilalis, 2018). For instance, Thomas et al. (2004) found that perennial species (e.g. *Cirsium arvense* and *Sonchus arvensis*) tend to dominate in direct

seedling systems while annual species (e.g. *Setaria viridis*) are associated with a range of tillage systems: from intensive conventional tillage to direct seedling systems. Similarly, Bilalis et al., (2001) showed that the abundance of annual species (e.g. *Stellaria media*) is high in conventional and reduced tillage systems, while perennials (e.g. *Malva sp.*) increase their abundance under direct seedling system. It has been suggested that the proportion of perennial weeds increases as tillage is gradually reduced from conventional tillage to direct seedling, since most annuals are adapted to cyclic soil disturbances (Gaba et al., 2017), and mostly recruit from soil seed banks (Auskalniene, Kadziene, Janusauskaite, & Suproniene, 2018; Shaukat & Siddiqui, 2004). Another explanation would be that herbicides are more effective against annuals than against perennials (Derr, 1994a), and the use of reduced tillage systems (or even conventional tillage) may help in managing herbicide resistant weeds that may characterize direct seedling systems (i.e. perennials); this is considered one of the emerging challenges especially in cereal cropping systems (G. A. Thomas, Titmarsh, Freebairn, & Radford, 2007). However, our results support the hypothesis of a species-specific response to soil preparation, as previously suggested by several studies (Blackshaw, 2004; Derksen, Lafond, Thomas, Loeppky, & Swanton, 1993; Tuesca, Puricelli, & Papa, 2001). The weak difference between reduced tillage and direct seedling in our study can also be explained by the fact that even the direct seedling system experiences cyclic soil disturbances at the time of harvesting, so that the soil disturbance regime may not strongly differ between the two systems (CHARLES L. Mohler, Liebman, & Staver, 2001).

3.6.2. Impact of cover crops

It is noteworthy that the use of *Camelina* as winter CC increases the relative abundance of several patrimonial species (e.g. *Coriandrum sativum*) at the expense of certain noxious species (e.g. *Cirsium arvense*), irrespectively to the type of soil preparation. As an intercrop, *Camelina* impacts the relative abundance of weed species in a way which is independent from the

biological type. Some perennials (e.g. *Artemisia vulgaris*) as well as some annuals (e.g. *Matricaria recutita*) are favored by *Camelina*, while some other perennials (e.g. *Cirsium arvense*) and annuals (e.g. *Atriplex patula*) are suppressed (see Fig. 3). In comparison, the winter CC-mix (Leguminosae-Brassicaceae) has a weak effect on the relative abundance of weed species, which further depends upon soil preparation. For example, *Coriandrum sativum* is favored in direct seedling plots only, while *Persicaria maculosa* is favored in reduced tillage plots only. This is consistent with several studies, where CCs were associated with lower weed abundances (i.e. higher soil fertility) (Drinkwater, Wagoner, & Sarrantonio, 1998; Plaza et al., 2015; Teasdale, 1996), though this suppressive effect is likely species-specific (Creamer, Bennett, Stinner, Cardina, & Regnier, 1996) and soil preparation-dependent (Shrestha, Knezevic, Roy, Ball-Coelho, & Swanton, 2002). Winter CCs are thought to exert a physical barrier against upward seedling growth since they have a head start over weeds that allows them to pre-empt space and resources before weeds and thus to outcompete them (Lawley, Teasdale, & Weil, 2012; Weber, Kunz, Peteinatos, Zikeli, & Gerhards, 2017). *Camelina* is believed to further impact weed germination via allelopathic effects, especially towards annual species (Leather, 1983; Massantini, Caporali, & Zellini, 1977).

In contrast with *Camelina* as a winter CC, the *Leguminosae-Brassicaceae* CC increases both weed diversity and yields of the cash crop (as measured via mean seed mass per stem of sunflower). These positive effects may be attributed to Leguminosae species which are well-documented for supplying nitrogen via their N_2-fixing symbiotic bacteria (Mazzoncini, Sapkota, Barberi, Antichi, & Risaliti, 2011; Rangel et al., 2017), increasing soil organic matter (Raphael, Calonego, Milori, & Rosolem, 2016), reducing soil compaction and erosion (Baumhardt, Stewart, & Sainju, 2015), improving the C:N ratio associated with microbial community (Frasier et al., 2016), and breaking up pest and disease cycles (Flint, 2018). Consistently, several studies indicated a CC-induced increase of crop yield when *Leguminosae*

are included (Snapp et al., 2005; Tonitto, David, & Drinkwater, 2006), while *Camelina* intercrops have been associated with lower crop yields (Gesch & Archer, 2013; Johnson et al., 2017).

3.7. Concluding remarks

Our study clearly shows that winter *Leguminosous-Brassicaceae* CC intercrop combined with direct seedling ensures higher weed diversity and sunflower yields than with reduced tillage or other soil cover types. On the other hand, *Camelina* as a monospecific intercrop ensures selective weed control towards less noxious weeds but more patrimonial, non-problematic weeds. As a CC, *Camelina* has the potential to allow reducing herbicide application (J. G. Crowley & Fröhlich, 1998; James Gerard Crowley, 1999). Its weak detrimental effect on sunflower yield is likely compensated by the fact that, as an oil seed plant, *Camelina* represents a second cash crop whose seeds have a high economic added value (Keske, Hoag, Brandess, & Johnson, 2013).

Both types of rotation thus meet the criteria of a sustainable agriculture. However, further work is needed to make sure that these results hold true on the long-term and to assess whether they can be retrieved for other cash crops or in other soil and climate contexts.

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AUTHOR CONTRIBUTIONS

G.D., F.D, J.L., A.A., and D.C. conceived the research idea as well as the analytical framework; A.A., F.S., B.B., F.D., O.C. and F.D. collected data in the field; A.A., F.S. and J.L. performed all statistical analyses; EGM provided maps and GIS support. A.A., with contributions from G.D., J.L., F.S., F.D., F.D., D.C and O.C., wrote the paper; all authors discussed the results, provided feedback, and commented on the initial version of the manuscript.

SUPPORTING INFORMATION

Appendix 3-1: Timeline of the different events occurring throughout the course of the experiment to prepare the right conditions for each of the eight studied treatments. Each of the eight treatments is repeated three times (i.e. three blocks).

Appendix 3-2: List of weed species used and sown at each of the 24 plots of the experimental site as well as for the three replicates in the greenhouse (cf. germination test).

Appendix 3-3: List of candidate models together with their corresponding AIC values for the three response variables studied. Y corresponds to weed abundance or weed richness or sunflower yield (weight of seeds/stem or height).

Appendix 3-4: Species germination percentage in the field versus the greenhouse. Extreme values (>100%) in the field are due to the seedbank effect

Appendix 3-5: Weed species richness and total abundance with the difference in soil preparation, soil cover rotation, block and date in the studied 24 plots.

Appendix 3-6: Abundance of weed species according to the block (A) and date (B) effects. Only the most abundant species are presented.

Appendix 3-7: Detailed outputs of the best candidate model selected (see M24 in Appendix 3-3 for the model formula) at the species level to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance individually (outcomes of the "manyglm" function from the "mvabund" package). Bold values represent significant ($p<0.05$) effects (A) and their corresponding coefficient estimates (B).

Appendix 3-8: Weed species relative abundance with the difference in soil preparation, soil cover rotation, block and date in the studied 24 plots.

Appendix 3-9: Difference in sunflower height (A) and weight of seeds per stem (B) at different soil preparations, soil cover rotations and blocks. Abbreviations in x-axis are for the three variables: CSN corresponds to *Camelina* and sunflower rotation without tillage (i.e. direct seedling). CST corresponds to *Camelina* and sunflower rotation with reduced tillage. COSN corresponds to CC-mix with sunflower rotation without tillage (i.e. direct seedling). COST corresponds to CC-mix with sunflower rotation with reduced tillage. NNN corresponds to the soil left without both winter and summer covers and without tillage (i.e. direct seedling). NNT corresponds to the soil left without both winter and summer covers and with reduced tillage.

NSN corresponds to soil left in winter and cultivated with sunflower as summer crop without tillage (i.e. direct seedling), and NST corresponds to soil left in winter and cultivated with sunflower as summer crop with reduced tillage.

Chapter 4: Hedgerows as corridors for forest plant species: A test for seed germination and plant establishment

4.1. Résumé

Les haies constituent un habitat potentiel pour les espèces végétales spécialistes des habitats forestiers. Néanmoins, la plupart des espèces forestières sont absentes des haies les plus récentes. Cette absence est potentiellement liée à la faible capacité de dispersion des espèces herbacées forestières ou bien à un faible succès de germination ou d'installation résultat de conditions biotiques et abiotiques dégradées par le fort effet « lisière » des haies récentes dont la canopée est peu développée et souvent immature, entrainant une forte compétition pour la lumière avec les espèces végétales plus généralistes des ourlets pré-forestiers. A l'aide d'une approche expérimentale, nous avons examiné si l'absence d'herbacées forestières au sein des haies les plus récentes était liée à une limitation à la dispersion ou bien à une limitation au recrutement (germination et installation). Le 12 avril 2018, nous avons semés et transplantés 17 et 13 espèces herbacées forestières, respectivement, le long de cinq transects de haies situées dans le nord de la France. Au sein de chaque transect et pour chaque espèce semée et/ou transplantée, deux modalités de perturbation ont été testées : une modalité non perturbée pour laquelle les graines et/ou les transplants ont été soumis à un effet de compétition avec la végétation résidente et une modalité perturbée avec retrait de la végétation résidente pour limiter la compétition avec les espèces héliophiles et nitrophiles des bords de haies. En tant que modalité de contrôle, les mêmes 17 et 13 espèces ont été semées et/ou transplantés, respectivement, le 22 Avril 2018 au sein d'un fragment forestier proche et suivant le même dispositif que celui utilisé dans les haies. Des observations de succès de germination des graines et/ou de survie des transplants ont été réalisés les 19 et 20 Juin 2018 pour les transects situés dans les haies et le 29 juin 2018 pour les transects situés en forêt. Nous avons utilisé des modèles linéaires généralisés avec effets mixtes pour analyser le succès de germination des graines et de

survie des transplants au sein du dispositif expérimental. Les résultats montrent des réponses spécifiques suivant l'espèce considérée. Certaines espèces sont clairement limitées par leurs faibles capacités de dispersion (p.ex. *Veronica hederifolia, Stellaria holostea*) tandis que d'autres ne germent pas (p.ex. *Fragaria vesca, Lamium galeobdolon*) ou ne s'installe pas (p.ex. *Hyacinthoides non-scripta).* Nos résultats confirment non seulement que les capacités de dispersion limités des espèces forestières sont bien une barrière importante mais ils suggèrent également que les conditions biotiques et abiotiques au sein des haies récentes jouent un rôle clé sur le succès de germination des graines semées et/ou d'installation des individus transplantés. Par conséquent, les conditions environnementales sub-optimales qui règnent au sein des haies récentes sont à prendre en compte en plus des barrières potentielles à la dispersion liées à la fragmentation de l'habitat forestier. Des recherches plus approfondies impliquant un gradient de conditions d'habitats allant de conditions dégradées (haies récentes) à des ambiances plus forestières (haies anciennes) seraient nécessaires pour évaluer le type de haies le plus optimal pour servir de corridors écologiques aux espèces végétales forestières.

Mots clés: haies vives, espèces herbacées forestières, germination, installation, végétation résidente.

4.2. Title

Hedgerows as corridors for forest plant species: A test for seed germination and transplant establishment

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This part corresponds to an ongoing experiment that needs further surveys in order to have more advanced results that support publication

ABSTRACT

Hedgerows are linear habitats that may provide optimal conditions for forest plant specialist species to establish if dispersal is not a limitation. Yet, very few forest herbs occur in recent hedgerows, potentially due to the very limited dispersal abilities of forest plants or due to the deteriorated biotic and abiotic conditions within recent hedgerows: strong edge effects due to the non-mature tree canopy leading to a fierce interspecific competition for light with the more generalist species inhabiting the recent hedgerows. By using an experimental approach, we examined whether the absence of forest plant species in hedgerows is due to dispersal or recruitment limitations. On 12 April 2018, we sowed and/or transplanted 17 and 13 forest plant species, respectively, across five hedgerows in northern France. Within each hedgerow, each plant species was sown and/or transplanted in both undisturbed and disturbed (i.e. vegetation removal) plots using a paired design to test for potential recruitment limitation due to competition with the resident vegetation. As a control, the same set of species were sown and/or transplanted on 22 April 2018 across 2 transects in a neighbouring forest patch and using the same paired design with both disturbed and undisturbed plots. Germination and/or establishment success were monitored on 19 and 29 June 2018 for both hedgerows and the neighboring forest, respectively, by counting the number of individuals that germinated and survived. Using generalized linear mixed-effects models, we analyzed the germination and persistence success, separately, by assessing the number of germinated (i.e. seeds) and/or the number of established (i.e. transplants) individuals of every species (response variables) as a function of habitat type (forest vs. hedgerow) and disturbance (with vs. without resident vegetation). We found species-specific responses in terms of germination and establishment success. Some species are clearly limited by dispersal (e.g. *Veronica hederifolia, Stellaria holostea*) while others do not germinate (e.g. *Fragaria vesca, Lamium galeobdolon*) or establish (e.g. *Hyacinthoides non-scripta*) inside recent hedgerows. Our findings suggest that not only

dispersal limitation matters for forest plant species to occur in the most recent hedgerows but also the quality of the habitat matters. The sub-optimal microclimate conditions within recent hedgerows, probably due to the immature tree canopy, contribute to the germination and establishment of forest herbs. Therefore, recent hedgerows may be considered as selective filters for forest plant species. Not only dispersal limitations matter for forest plant species to colonize hedgerows but also environmental conditions therein matter for the effective migration of forest herb specialists. Further investigations involving a gradient of hedgerows' habitat quality ranging from poor (recent hedgerows) to good (ancient hedgerows) may provide important answers on the most optimal type of hedgerows that is required as effective corridors for forest herbs.

Keywords: *dispersal, establishment success, forest plant species, germination, persistence, hedgerows, resident vegetation.*

4.3. Introduction

Forest fragmentation due to anthropogenic disturbances is a widespread phenomenon in agricultural lowlands of northwestern Europe, resulting in habitat loss and degradation (Mortelliti et al., 2011). The meta-community dynamic of forest plant species within small and isolated forest fragments is therefore potentially disrupted (Decocq et al., 2016). Indeed, forest plant species will not only suffer from habitat degradation but also from the absence of corridors connecting forest patches. Consequently, herbaceous forest plant species may face higher extinction risks with potential cascading effects on the higher trophic levels (Valiente-Banuet et al., 2015). Restoring the connectivity among forest habitats within anthropogenic landscapes of northwestern Europe is a priority to ensure sustainability in ecosystem functioning and thus the delivery of ecosystem services.

Hedgerows are called the 'green veins' of agricultural landscapes by European researchers and are defined as linear elements of shrubs and trees being 20-m long, at least, and less than 5-m wide (Bickmore 2002). During the last decades, several ecologists suggested the idea that hedgerows are potential habitats for forest species and a mean of connectivity between forest fragments. Several studies have shown that hedgerows may be a suitable habitat for forest herbaceous plants and have other benefits for nearby landscapes (Fahrig & Merriam, 1994; Henein & Merriam, 1990). A study from Italy has shown that hedgerows within agricultural landscapes may act as effective corridors for forest plant species (Sitzia, 2007). Interestingly, Corbit et al. (1999) stated that about 40% of forest herbs are encountered in hedgerows in Central New York (USA) and that richness of forest herbs as well as similarity of composition to neighboring forest declines with distance along the hedgerow from forest. This idea that hedgerows are efficient habitat corridors for forest herbs is supported by the study of Petit et al. (2004), who showed that the number of forest plant species is greater in hedgerows connected to woodlands. Freemark et al. (2002) have also demonstrated that hedgerow networks within

agricultural landscapes may act as protected areas for the conservation of endangered species. However, other studies stated that hedgerows are frequently disturbed by human activities with negative impacts on the quality of the habitat therein, such that forest plant species are unlikely to use disturbed hedgerows as corridors for migration throughout the landscape (Honnay, Hermy, & Coppin, 1999; Klaus et al., 2015). Several comparative studies have recorded a decline and higher mortality rates of forest plant species in hedgerows (Cunningham, 2000; Schmucki & de Blois, 2009) than in forests. Furthermore, a study that was performed in Canada and which involved the transplanting of forest plant species in hedgerows revealed unsuccessful establishment and showed that hedgerows are unsuitable habitats for forest plant species (Fritz & Merriam, 1993). Other ecologists have an intermediate theory for which hedgerows are considered as potential corridors for specific forest plant species depending on spatiotemporal connectivity (Françoise Burel & Baudry, 1990; Forman & Baudry, 1984). Thus, whether hedgerows are efficient corridors for forest plant species remains an open question.

Forest specialist species are often absent from the most recent hedgerows, but are present in ancient hedgerows. This can be explained by time lags due to the poor dispersal abilities of forest plant species (sown seeds will germinate and potentially establish) (H1) and/or by the inadequate quality of the habitat within recent hedgerows which may limit recruitment (sown seeds will not germinate) due to unsuitable abiotic (H2; e.g. unfavorable microclimate soil conditions due to pollution from adjacent land uses) or biotic (H3; competition for light with the resident vegetation community dominated by generalist species) conditions, or even limit establishment of transplants if germination is not a limitation (H4; persistence limitation). Using a controlled experiment, we examined which forest species available within the regional species pool of forests plant species are able to germinate and establish in recent hedgerows (about 20-yr old).

To test these four hypotheses, we performed three parallel experiments at three different locations:

1) Hedgerow treatment: a total of 17 and 13 forest plant species were sown and transplanted, respectively, along several transects located within five recent hedgerows surrounded by agricultural fields.
2) Forest control: the same "control" experiment was performed in a neighboring forest where the same set of forest plant species were sown and transplanted along transects.
3) Greenhouse germination test: the 17 studied forest plant species were sown in a controlled greenhouse experiment to test the germination success of each species.

4.4. Materials and Methods

4.4.1. Study area and site characteristics

We conducted our experiment in very recent hedgerows (age between 20 and 22 years) located in northern France (Marcelcave; latitude: 49.85° North; longitude: 2.574° East; altitude: 75m a.s.l.). The control forest site was located in a neighboring forest south of Amiens (latitude: 49.88° North; longitude: 2.293° East; altitude: 35m a.s.l.) (Fig. 4-1). The climate is oceanic with monthly precipitation (659mm, on average) regularly distributed throughout the year and monthly mean temperatures ranging between 2.6°C (January) and 17.6°C (July). The soil is primarily of luvisol type.

4.4.2. Study design

We selected a set of five recent hedgerows that can be considered as 5 replicates. For each of the five hedgerows, we set up 2 transects: one for testing seed germination (17 species) and one for testing transplant survival (13 species) (Fig. 4-1a & Table 4-1). For each species within each transect, 2 sets of seeds and transplants were used to test the potential effect of competition with the resident vegetation community: one set was directly sown/transplanted without disturbing the resident vegetation to test the effect of competition (i.e. non-disturbed) and the other set was sown/transplanted after removing the resident vegetation to avoid competition (i.e. disturbed) (Fig. 4-1c). Note that all selected hedgerows are more or less parallel and perpendicular to the nearby road with a linear orientation towards the north. The hedgerows were composed of shrubs and full-grown trees, with a width of 2 to 4 meters.

Inside the control forest site, four separated transects were installed (Fig. 1b), where two transects were used for seed sowing (17 species) and the two other transects for the transplant experimentation (13 species). The same set of species was used in the forest transects and the hedgerows and the disturbance treatment was also tested within the control forest site (i.e. disturbed vs. non-disturbed).

Table 4-1: List of species used for the germination *(with the respective number of seeds per sub-quadrat indicated in parenthesis: the mean across all species and its associated standard deviation equals 44.76 ± 9.21) (A) and transplant (with the respective number of transplants per sub-quadrat indicated in parenthesis: the mean across all species and its associated standard deviation equals 8.82 ± 1.82) (B) experiments.number*

Species	
A) Germination test	**B) Persistence test**
Aegopodium podagraria (50)	*Aegopodium podagraria (7)*
Carex sylvatica (50)	*Anemone nemorosa (10)*
Circaea lutetiana (20)	*Carex sylvatica (6)*
Fragaria vesca (34)	*Fragaria vesca (6)*
Galium odoratum (50)	*Galium odoratum (9)*
Hyacinthoides non-scipta (50)	*Hyacinthoides non-scipta (10)*
Lamium galeobdolon (50)	*Lamium galeobdolon (10)*
Lapsana communis (50)	*Melica uniflora (9)*
Melica uniflora (50)	*Oxalis acetosella (10)*
Milium effusum (50)	*Stellaria holostea (10)*
Oxalis acetosella (30)	*Veronica hederifolia (10)*
Poa nemoralis (45)	*Viola reichenbachiana (5)*
Senecio ovatus (50)	
Stachys sylvatica (50)	
Stellaria holostea (50)	
Veronica hederifolia (32)	
Viola reichenbachiana (50)	

Along each transect in both habitat types (forest and hedgerows), every species was sown and/or transplanted within quadrats of 50cm × 50cm each, further divided into two equal parts (sub-quadrats) of 20cm × 50cm each (Fig. 4-1c): one for the non-disturbed (competition) treatment and one for the disturbed (vegetation removal without competition) treatment. Both sub-quadrats were separated by a buffer area of 10cm × 50cm (see Fig. 4-1c). Each sub-quadrat of 20cm × 50cm was further divided into 10 equal units of 10cm × 10cm each. About 3-5 seeds were sown per 10cm × 10cm unit while only one single individual was transplanted per 10cm

× 10cm unit. Note that, for some species, we had less than 10 individuals transplanted within a given sub-quadrat (see Table 4-1b).

4.4.3. Seed collection and preparation

In 2017, we collected seeds for 17 forest plant species (Table 4-1a) by regularly visiting forest stands around Amiens. Seeds were extracted on mature plants, dried and further divided into 17 different seed sets (5 hedgerows × 2 disturbance treatments + 2 forest transects × 2 disturbance treatments + 3 sets for the greenhouse germination test) per species, each Eppendorf tube containing about 30 to 50 seeds. Seeds were counted using SCM-C automatic seed counting machine (BR Biochem Life Sciences Pvt. Ltd). For very small seeds, we used a stereoscope to identify individual seeds and get a precise count.

4.4.4. Transplant collection

On April 12th and 22nd 2018 for the hedgerows and the forest control site, respectively, we visited forest stands around Amiens and collected fresh transplants for 13 different forest species (Table 4-1b). When possible, a total of 140 transplants per species were collected: 10 transplants × (5 hedgerow's transects + 2 forest's transects) × 2 (one for the disturbed level and one for the non-disturbed level). The time interval between collecting the transplants in the field and moving them to both the hedgerows and the control forest site was less than 2 hours. Transplants' roots during this interval were kept humid so that they are planted fresh in their corresponding destination.

4.4.5. Timeline of the experiment

On April 12th 2018, we sowed the seeds and installed the transplants along each of the five hedgerow's transects at Marcelcave (Fig. 4-1). For each transect, a total of 29 quadrats of 50cm × 50cm each (17 quadrats for the seed experiment and 13 quadrats for the transplant experiment) were installed on that day. For the two transects located in the forest control site

near Amiens (Fig. 4-1), seeds and transplants were sown and transplanted on April 22nd 2018 following the same protocol as for the hedgerow's transects (17 quadrats of 50cm × 50cm each for the seed experiment and 13 quadrats of 50cm × 50cm each for the transplant experiment).

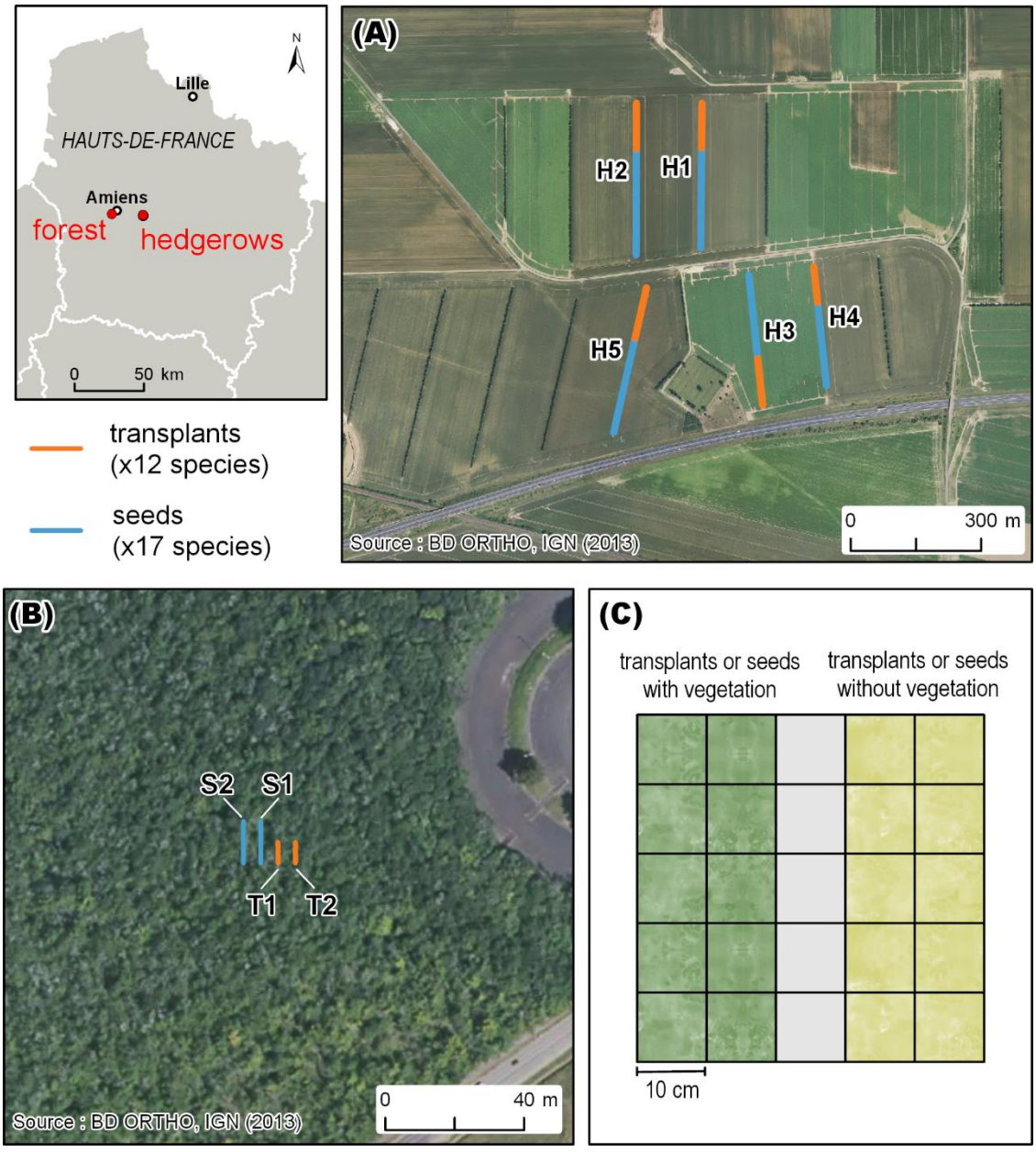

Figure 4-1: Map of the study area (Hauts-de-France) *covering two different regions:* ***(A)*** *Marcelcave for hedgerows; and* ***(B)*** *the forest experimental site near Amiens as a control. Five isolated and recent hedgerows (H1-H2-H3-H4-H5) were used to install the five transects containing both the seed and transplant quadrats (17 and 13 quadrats per hedgerow, respectively). Four separated transects were used in the experimental forest near Amiens: two transects were installed for the seed quadrats (S1 and S2) and two others were installed for the*

*transplant quadrats (T1 and T2). For each of the nine transects (hedgerow and forest transects), every single quadrat of 50cm × 50cm is divided into two sub-quadrats of 20cm × 50cm each, where the right sub-quadrat is the disturbed or vegetation removal treatment and the left sub-quadrat is the non-disturbed treatment or competition treatment separated by a 10cm × 50cm buffer zone **(C)**.*

In late April 2018, three replicates of the 17 species that were sown in hedgerows and the forest control site were also sown in the greenhouse and monitored for 3 months using a direct germination method. The seed mixtures were spread over steam-sterilized compost-filled containers and allowed to germinate in the greenhouse under a natural light regime and a temperature regime ranging from 25°C during the day and 20°C during the night. The containers were kept moist by regular watering. Three control containers containing only steam-sterilized compost without seeds were distributed among the other containers to detect eventual contamination from either airborne propagules or propagules present in the potting soil. No contamination was detected. The emergence method was preferred because we were interested in viable propagules. All identified seedlings were counted and removed, while unidentified seedlings were transplanted and identified upon flowering. Seedling emergence was checked from May 2017 until July 2018, at weekly intervals.

Hedgerows and the forest control site were surveyed on June 18th and 29th 2018, respectively, and the abundance (number of individuals) of each forest plant species was recorded within each sub-quadrat of 20cm × 50cm.

4.4.6. Data analysis

Based on our experimental design, we built a list of candidate models (Table 4-2) to test the separate effects of habitat abiotic conditions (hedgerows *vs*. forest) and competition (disturbed *vs.* un-disturbed) on the proportion of individuals which successfully germinated or established within a given 20cm × 50cm sub-quadrat (i.e. the response variable). The two-way interaction between habitat conditions and competition level was also tested. Given that the response

variable is a proportion data with many zeroes, we used generalized linear mixed-effects models with a zero-inflated distribution and a binomial family. Transect ID (H1, H2, H3, H4, H5, F1, F2) was used as random intercept term and species name was set as a random variable interacting with the fixed effect variables depending on the studied model (random slope terms, see Table 4-2). For each candidate model, we computed the Akaike Information Criterion (AIC) with the best model being the one with the lowest AIC value (Burnham & Anderson, 2002). Once the best candidate model was selected, we extracted the coefficient estimates, standard errors and associated p-values for each of the predictor variables listed in the best model. Finally, we extracted, for each species, the estimated mean and 95% confidence interval of the estimated relative proportion of seeds/transplants that germinated/established.

Table 4-2: List of candidate models used *to test the separate effect of competition (with vs. without resident vegetation) and habitat type (forest vs. hedgerows) on both the germination (MG) and establishment (ME) success. The response variable in all models is the proportion of individuals that germinated or successfully established. Generalized linear mixed-effects models with zero inflated distribution (glmmTMB) were used.*

Symbol	Candidate Model	AIC
MG1	Y ~ competition (Y/N)	220.57
MG2	Y ~ habitat (H/F)	154.67
MG3	**Y ~ competition (Y/N) + habitat (H/F)**	**147.95**
MG4	Y ~ competition (Y/N) * habitat (H/F)	164.02
ME1	Y ~ competition (Y/N)	544.27
ME2	Y ~ habitat (H/F)	543.25
ME3	Y ~ competition (Y/N) + habitat (H/F)	523.11
ME4	**Y ~ competition (Y/N) * habitat (H/F)**	**517.65**

All statistical analysis were performed using the "nlme", "ggplot2", "Matrix", "reshape2", "mvtnorm", " lme4", "gridExtra" and "glmmTMB" packages in the R software environment version 3.4.1 (R Core Team 2017).

4.5. Results

Most forest herbs, except for *Veronica hederifolia* and *Stellaria holostea*, did not germinate in the hedgerows (Fig. 4-2A). For the forest control site, only four species (*Aegopodium podagraria, Stachys sylvatica, Fragaria vesca, Lamium galeobdolon*) germinated (Fig. 4-2A). In the greenhouse experimentation for the same set of species (17 species with the same number of inserted seeds per species, see Table 4-1), six species succeeded to germinate (*Veronica hederifolia, Lapsana communis, Milium effusum, Stellaria holostea, Poa nemoralis, Fragaria vesca,* see Appendix 4-1 for the number of germinated individuals per species). The best candidate model explaining species germination success (dispersal limitation) included habitat conditions (hedgerows *vs*. forest) and competition (disturbed *vs.* un-disturbed) as predictors without the interaction term (MG3 in Table 4-2). Neither habitat type not competition level had a significant effect on the germination success of the tested species, albeit we found a tendency ($p=0.17$) towards lower germination rates in hedgerows as opposed to forest conditions (Table 4-3).

The best candidate model explaining transplants' establishment success (recruitment limitation) included the interaction term between habitat conditions (hedgerows *vs*. forest) and competition (disturbed *vs.* undisturbed) (ME4 in Table 4-2). We found a clear significance ($p<0.05$) in the studied model (Table 4-4) for the interaction term between habitat conditions and competition with better establishment rates in the hedgerows with vegetation removal (no competition) as opposed to forest conditions without vegetation removal. When studying the behavior of every species separately in both cases (seed and transplant experiment), *Veronica hederifolia* and *Stellaria holostea* appear to be favored in both the disturbed (without vegetation) and the non-disturbed zone (with vegetation) of hedgerows, while all other remaining species recorded no difference between forest and hedgerows. For transplants, it appears that most (nearly nine out of the thirteen) species succeeded to establish in hedgerows

with even greater success rates than in forest, especially so after removal of the resident vegetation (i.e. no competition) (see Fig. 4-2 & Fig. 4-3).

Table 4-3: Outputs from the best candidate model of the germination (seeds) success of forest plant species *under two different habitat types (forest vs. hedgerows) and two disturbance regimes (with resident vegetation vs. without resident vegetation). Generalized linear mixed-effects models with zero inflated (glmmTMB) and a binomial family were used to relate species abundance (proportion of individuals that successfully germinated or established) with the predictor variables. Bold values are representing significant (p<0.05) effects.*

Term	Estimate	Std. Error	z value	Pr(>|z|)
Intercept (forest w/ vegetation)	-7,6493	2,0592	-3,7147	0,0002
Disturbance (w/o vegetation)	-0,3655	0,4434	-0,8242	0,4098
Habitat (hedgerow)	-8,1168	5,8853	-1,3792	0,1678

Table 4-4: Outputs from the best candidate model of the establishment (transplants) success of forest plant species *under two different habitat types (forest vs. hedgerows) and two disturbance regimes (with resident vegetation vs. without resident vegetation). Generalized linear mixed-effects model with zero inflated (glmmTMB) and a binomial family were used to relate species abundance (proportion of individuals that successfully germinated or established) with predictor variables. Bold values are representing significant (p<0.05) effects.*

Term	Estimate	Std. Error	z value	Pr(>|z|)
Intercept (forest w/ vegetation)	-4,4091	0,6882	-6,4067	1,49E-10
Disturbance (w/o vegetation)	0,6167	0,9810	0,6287	0,5296
Habitat (hedgerow)	**2,7201**	**0,9732**	**2,7950**	**0,0052**
Distur.:Habitat (hedgerow w/o vegetation	**0,9504**	**1,0675**	**-0,8903**	**0,03733**

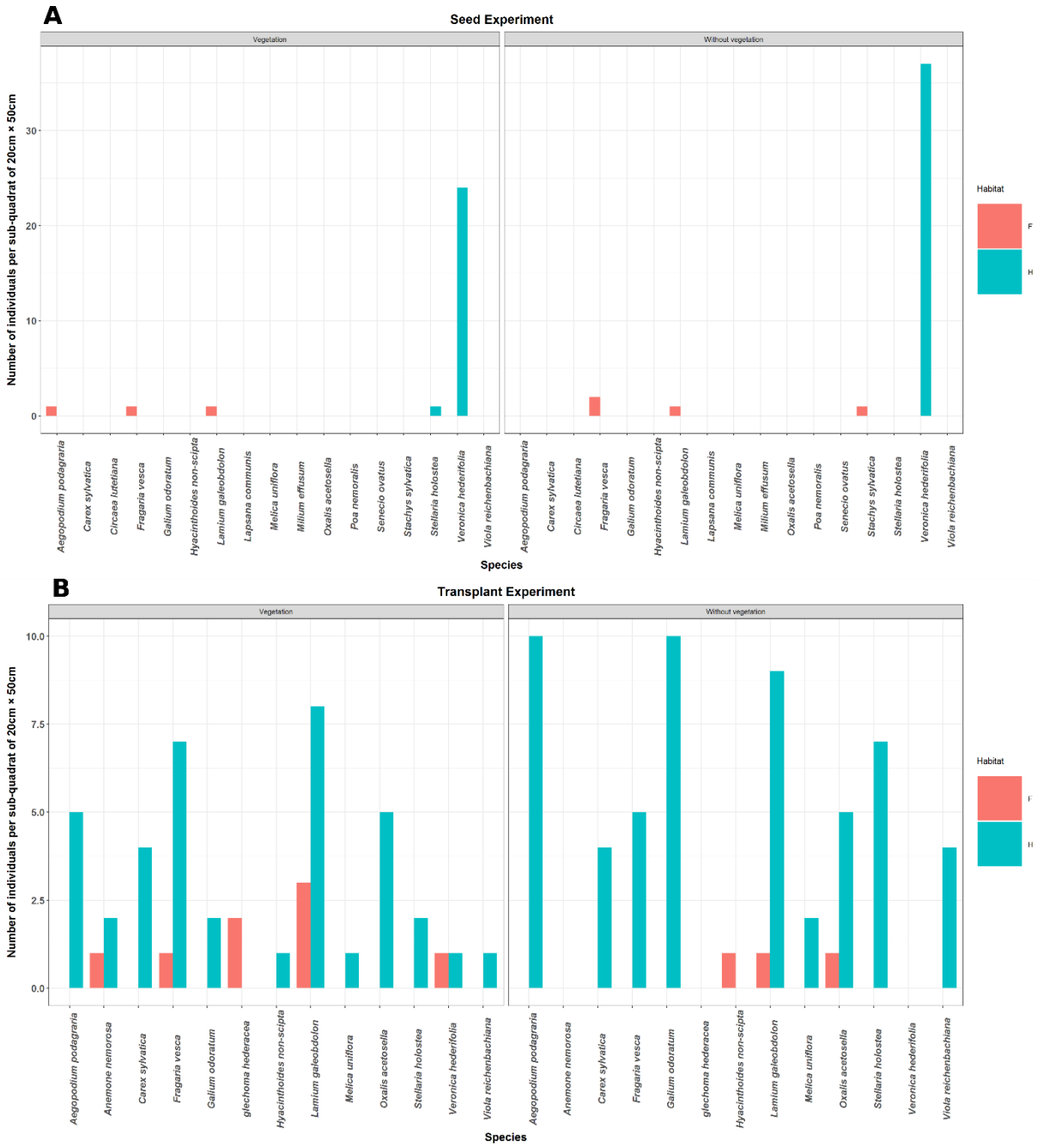

Figure 4-2: Seed germination success *in both forest (orange bars) and hedgerows (blue bars) of the 17 sown species* ***(A)*** *and* ***establishment success*** *in both forest (orange bars) and hedgerows (blue bars) of the 13 transplanted species* ***(B)***.

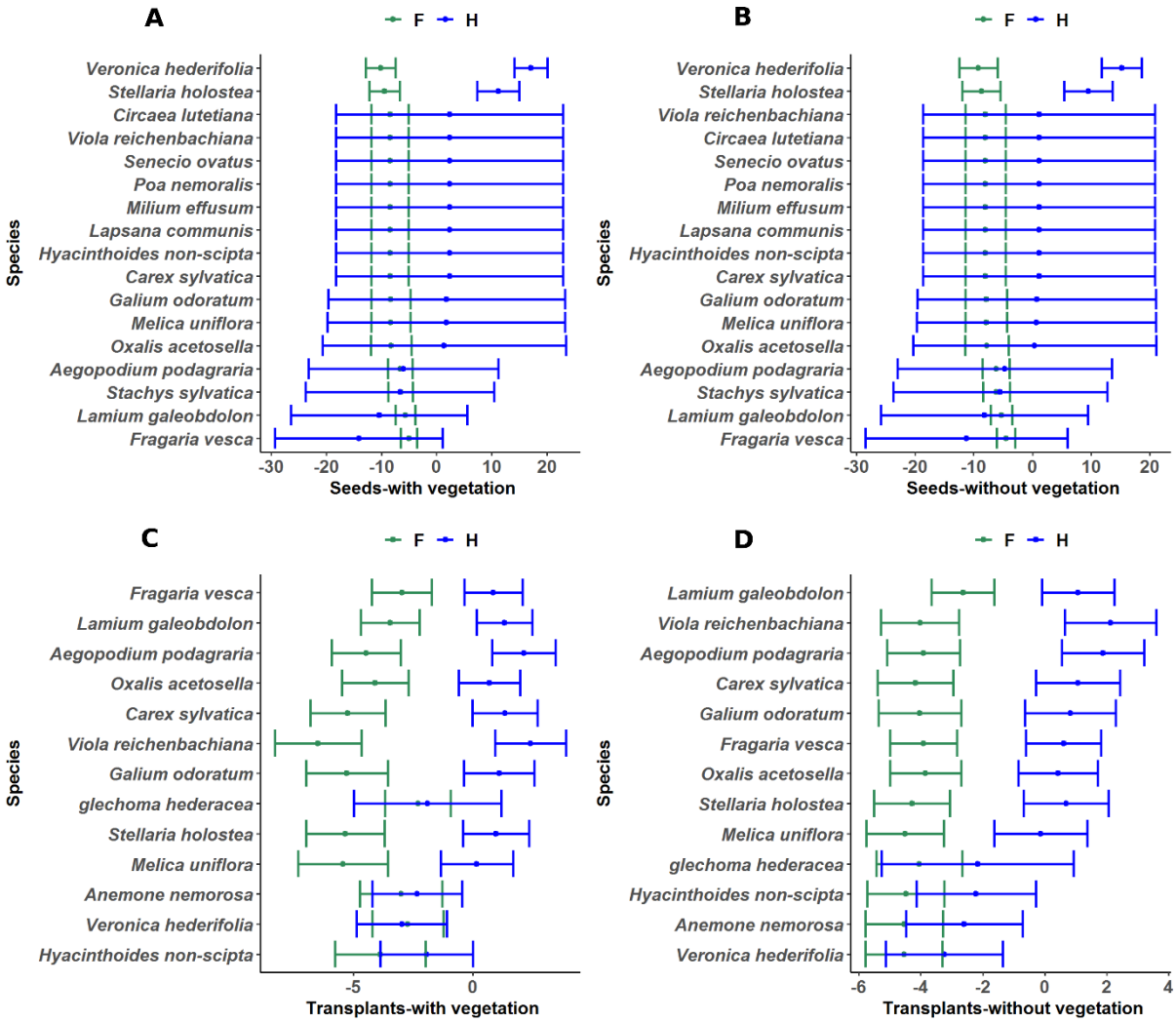

Figure 4-3: Estimated mean (effect size) and 95% confidence interval for each species separately. *Coefficients were extracted from the two best candidate models to test the effect of habitat conditions (hedgerows vs. forest) and competition (with vs. without resident vegetation) on the germination (seeds) and establishment (transplants) success of several forest plant spcies (see models MG3 for* ***A*** *&* ***B****, and ME4 for* ***C*** *and* ***D*** *in Table 4-2). The habitat condition differences at the species level are given for both seed germination success* ***(A****,* ***B)*** *and transplant establishment success (****C****,* ***D****). results are displayed separately for the two tested comeptition levels: with (****A****,* ***C****) and without (****B****,* ***D****) resident vegetation.*

4.6. Discussion

In our results, two forest species succeeded to germinate within hedgerows (i.e. *Veronica hederifolia & Stellaria holostea*), which suggests that both species are limited by their dispersal ability and thus would be able to germinate within hedgerows if dispersal was not a limitation. This validated H1, at least for these two forest species. In addition, the germination success of *Veronica hederifolia* and *Stellaria holostea* appears to be greater in hedgerows than in forest, regardless of the competition level which consequently drops out H3 for these two forest herb species which seem to be unaffected by competition with the resident vegetation. Concerning the transplant experiment, nine out of the thirteen studied forest plant species succeeded to establish in hedgerows, while the other four species (*Hycanthoides non-scripta*, *Anemone nemorosa, , Glechoma hederacea* and *Veronica hederifolia*) showed limited establishment in hedgerows either with or without resident vegetation. This suggests that H4 does not hold for most of the tested species that were able to persist within hedgerows. Noteworthy, we found a significant interaction effect between habitat conditions and competition, suggesting that the transplants of the tested forest herbs tend, in general, to better establish in hedgerows without the resident vegetation. This supports H3 and the general idea that biotic conditions may impede forest herb establishment within hedgerows.

Huseyinoglu (2017) and McCarthy (1994) explained that most forest plant species are stress-tolerant, but only species combining both stress tolerance strategy and competitive strategy are encountered in hedgerows. This is also supported by Hermy et al., (1999) who have found that ancient forest species with both stress-tolerant and competitive strategies are more abundant than other forest plant species. Species dispersal ability and immigration process contribute to the abundance of species in hedgerows (Henry Allan Gleason, 1917). Several studies explained that forest plant species are very limited by their dispersal abilities (Flinn & Vellend, 2005; Jacquemyn, Butaye, & Hermy, 2003). This may be due to their relatively large

seeds, presence of dispersal vectors with short-distance behaviors (dispersal by ants), short seed dormancy period, low recruitment rate and long pre-reproductive rate (Verheyen et al., 2003; Whigham, 2004). In case of hedgerows, continuous hedgerows attached to forests are considered suitable for forest plant migration and thus are considered as efficient corridors (Brunet & Oheimb, 1998; Tang, Liang, Lu, & Ding, 2014). However, with increased distance from the forest, isolated hedgerows will record lower forest species richness and abundance (Brunet & Oheimb, 1998). Eriksson (1996) explained the relationship between dispersal ability and persistence over time where it was summarized that species presence in a certain habitat depends on seed source availability, space and time of dispersal process, and life history characteristics of individual species.

Forest plant species colonizing new sites (e.g. hedgerows) also depends on the biotic conditions of the hedgerow itself, and more precisely its quality regarding microclimatic and soil nutrient conditions. Nutrient status of the soil and especially lower phosphate levels will make hedgerows unsuitable for some forest plant species to establish. Consequently, competitive and generalist plants occurring in both open and forest habitats will affect ancient forest species occurring in hedgerows throughout nutrient competition (Hermy et al., 1999). Corbit et al., (1999) stated that although there is a similarity in forest herb species composition between hedgerows and woodlands, several forest plant species do not occurr in hedgerows. Other studies had found that there are some forest herbs that are unique to woodlands and the associated edges without being present in hedgerows (Boutin & Jobin, 1998; Fritz & Merriam, 1993; Jobin, Boutin, & DesGranges, 1997). Several other variables may affect the presence of forest herbs in hedgerows such as the hedgerow width (Corbit et al., 1999; Sitzia, 2007), the presence of ditches in hedgerows, the age of the studied hedgerows and the associated microclimate. For instance, ancient hedgerows are known to harbor a higher richness of forest plant species (Closset-Kopp et al., 2017) compared with more recent hedgerows like the one

we studied here. This calls for more research to investigate whether germination and establishment successes would be enhanced in ancient hedgerows, where microclimatic conditions are closer to forest habitats, compared with recent hedgerows. In addition, the forest habitat we used in our experiment is considered a recent forest which may cause differences in terms of germination and establishment of forest plant species when compared to ancient mature forest habitat.

4.7. Conclusion:

The results of our study imply that most of the forest herb species we studied here (e.g. *Fragaria vesca, Melica uniflora*) are limited by the hedgerows' habitat (mostly abiotic) conditions (H2 verified) rather than being limited by their dispersal abilities (H1 rejected) while others (e.g. *Veronica hederifolia*) seem to be rather limited by their dispersal abilities (H1 verified). Concerning transplants, it appears that most of the species used in this study do succeed in establishing (H4 rejected) within hedgerows, especially so after the resident vegetation has been removed (no competition) (H3 verified).

The main limitation for forest plant species to occur within hedgerows is not only due to dispersal limitations but maybe also due to seed germination failure. Indeed, transplants were showing quite a good establishment success within hedgerows, which may be confirmed with further series of surveys. Very few seeds managed to germinate suggesting two interpretations: (1) either the seeds were not good enough and not viable where only six species (out of 17) succeeded to germinate in the greenhouse leaving behind a certainty about the quality of seeds. (2) or the microclimatic conditions (soil moisture and temperature) within both hedgerows and forest are unsuitable to break dormancy and allow the seeds to germinate starting from the fact that both habitats (forest and hedgerows) are considered recent, and eventually will record microclimatic conditions and soil properties that are different from the conditions and properties recorded in ancient forests (optimal habitat for germination and establishment of herbs). We

should keep in mind that this is an ongoing long-term study (3 years) and our current results are representing the first survey of the study (3 months after sowing the seeds and transplanting the transplants). With further series of surveys and more advanced analysis, it will be more promising to have a clear idea about the change in the behavior of forest species between both forest and hedgerows and discuss the idea of hedgerows being potential corridors for forest plant species.

SUPPORTING INFORMATION

Appendix 4-1: Greenhouse germination test for the 17 studied species (same species mix used to study germination success in both forest and hedgerows)

Chapter 5: General discussion, conclusions & perspectives

5.1. Background

The neutral theory is often invoked to explain famous macroecological patterns (McGill et al., 2007) for plants such as the species abundance distributions (SADs), describing the rarity and commonness of species in a certain community (Baldridge, Harris, Xiao, & White, 2016), and the species-area relationships (SARs) describing the non-linear increase in species richness as sampling area increases (Cencini, Pigolotti, & Muñoz, 2012). However, the idea of assuming that all plant individuals show equal fitness was criticized by many studies stating that neutrality is a "fragile" theory in the context of ecological equivalence (He, Zhang, & Lin, 2012; Zhou & Zhang, 2008). These studies suggested that species are different in their competitive ability, with competition being inevitable, giving rise to macroecological patterns that are quite different from the patterns predicted by the neutral theory. Therefore, earlier and recent studies explained species abundance and coexistence as a mean of studying the difference between "neutral" and "niche" theories based on both dispersal and recruitment processes (Hubbell, 2001).

Community structure, function and composition are controlled by multiple mechanisms, which include dispersal and recruitment. Both are considered key processes for plant community assembly (Fig. 5-4) and for maintaining the biodiversity in plant communities. Despite our experiments aiming to overcome dispersal limitations (**Chapters 3 and 4**), the germination success of some species is still not guaranteed (Clark et al., 1999), suggesting that dispersal limitations are not the only limitations explaining the absence of some plant species within the community. In addition, when overcoming both dispersal and germination limitations (**Chapter 4**), the success of plants to persist may not be achieved (Benítez-Malvido & Martínez-Ramos, 2013). Thus, studying both processes in different types of landscapes (e.g.

forests, hedgerows and agricultural fields) can provide insights about the challenges for maintaining diversity in plant communities and associated ecosystem services.

This thesis addresses a fundamental research question in ecology, especially in the current context of habitat alterations by anthropogenic activities: how are the spatio-temporal dynamics of plant species influenced by an interplay between plant species dispersal from one side, and environmental conditions along with species competitive abilities from the other side. The presence of a target plant species in a given community depends upon its niche requirements and dispersal capacities after accounting for the resilience of the ecosystem when both stochastic and deterministic anthropogenic disturbances occur (e.g. habitat fragmentation). Indeed, the resilience of ecosystems (i.e. their ability to maintain optimal functioning despite disturbances) is based upon the occupation of ecological niches, and upon the ability of species to modify their niche or adapt (i.e. recruitment) and move in space (i.e. dispersal) to track their shifting habitat envelopes. Therefore, community assembly rules control the presence of plant species and reflect the patterns of plant community structure. The different parts of this thesis allowed us to evaluate the extent by which community assembly processes may predict local plant species abundance (**Chapters 3 and 4**), influence the community structure from regional (gamma-scale) to local (alpha-scale) plant species pools (**Chapter 2**), and eventually predict the fate of plant community components. The results of this thesis demonstrate several important ecological advances:

1) Community assembly processes may show contrasting impacts on forest plant species richness patterns when forest habitats are fragmented, which depends on species affinity to forest habitats (i.e. specialists vs. generalists) (**Chapter 2**).
2) Forest specialists would rather have better fitness in a single large forest, while generalists are favored to maintain their fitness in several small forest patches (SLOSS

debate in **Chapter 2**), with an important impact of connectivity between forest patches on the assembly processes of plant communities.

3) Biotic interactions and abiotic conditions both interfere with the germination of plant species (e.g. competition) and the coexistence with other species (**Chapters 3 and 4**), with recorded different abundances and crop yields in agro-ecological systems (**Chapter 3**).
4) The absence of forest herb species within recent hedgerows seems to be mainly due to seed germination failure rather than dispersal limitation or unsuitable environmental conditions for the species to persist once they germinated.

5.2. SLOSS: the debate of habitat conservation strategies

Overall, it is rare to find a perfect nestedness across plant communities throughout the whole world (Berglund & Jonsson, 2003; Fischer & Lindenmayer, 2005). In a perfectly nested system, species will occur in a pattern so that small assemblages are considered a perfect subset of the larger assemblage into which it is embedded. Nestedness can result from differential dispersal abilities (McAbendroth, Foggo, Rundle, & Bilton, 2005) and from differential habitat quality (Hausdorf & Hennig, 2003; Hylander, Nilsson, Gunnar Jonsson, & Göthner, 2005). A study by Gonzalez, Rayfield, & Lindo, (2011) and another study from Lindo, Winchester, & Didham, (2008) on community nestedness stated that both species tolerance to environmental conditions in combination with species dispersal capacities account for the non-random compositional patterns of the studied communities. In studying the patterns of dissimilarity among communities, nestedness together with species turnover are the two main components driving beta-diversity or the dissimilarity among communities (Harrison, Ross, & Lawton, 1992; Lennon, Koleff, Greenwood, & Gaston, 2001; Williams, 1996). Regarding the gain and loss of species richness, both nestedness and species turnover are believed to be important components in discussing the SLOSS (single large or several small) debate in conservation ecology

(Diamond et al., 1976; Honnay, Hermy, Coppin, & P, 1999; D. S. Simberloff & Abele, 1976; Wright & Reeves, 1992).

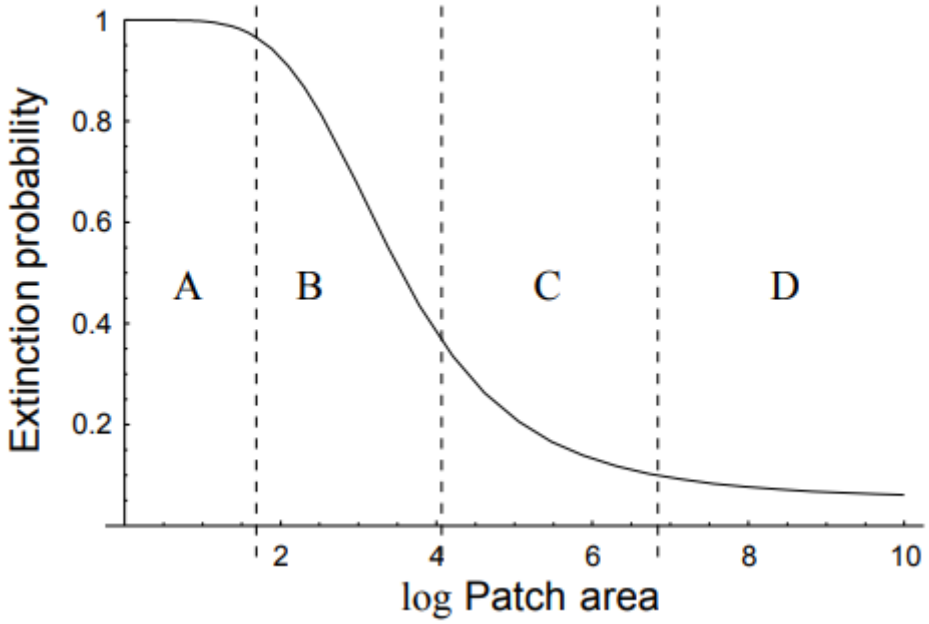

Figure 5-1: Hypothetical plot showing the probability of local extinction with respect to a wide range of patch areas. *The Letters from* ***(A)*** *to* ***(D)*** *represent patches of different sizes suggesting different local extinction risks. Extracted from Ovaskainen, (2002).*

In **Chapter 2**, we demonstrated that single large forests are more suitable for forest specialist species that are threatened by intensive practices and the instability of the environmental (without threatening generalist species but with less total species richness). In contrast, in small forest fragments, plant species richness may increase because there are more generalist species, but at the same time the extinction risk of forest specialist species increases. Our findings thus support conclusions from Quinn & Harrison (1988)' that small, isolated forest patches show higher species than both small less-isolated and larger forest patches. Other studies (e.g. Rybicki, Abrego, & Ovaskainen, 2018) have tested the "habitat amount hypothesis" proposed by Fahrig (2013), which states that fragmentation reduces alpha diversity but slightly increases gamma diversity in case of low habitat amount. Although our results are consistent with the "habitat amount hypothesis", this hypothesis received both support

(Arnillas, Tovar, Cadotte, & Buytaert, 2017; De Camargo, Boucher-Lalonde, & Currie, 2018) and opposition (Nick M. Haddad et al., 2017). Diamond (1976) had stated in his study about the "rules" for designing protected areas based on the theory of "Island biogeography" of Wilson & MacArthur, (1967) that the best system in the SLOSS debate is the single large reserve, while Simberloff, (1982) went in his encouragement towards the several small reserves. In fact, the SLOSS debate cannot be resolved easily since the two approaches depend on different circumstances and the focal species. Single large reserve may be useful for specialist species (Burkey, 1999), whereas several small reserves will enhance gamma diversity at the regional level but at the expense of the most patrimonial or specialised species (Hufbauer et al., 2015) (Fig. 5-1).

5.3. Importance of habitat connectivity

In metapopulation ecology, site isolation will affect both colonization rates (Moilanen & Hanski, 1998a; Wilson & MacArthur, 1967), and the probability of a "rescue effect" (Brown & Kodric-Brown, 1977b). With increased anthropogenic inputs, landscapes are subjected to a wide range of conversions and increased in habitat loss and fragmentation (Nicol & Possingham, 2010). To overcome the subsequent biodiversity loss due to habitat loss and habitat fragmentation, ecologists have highlighted the importance of connectivity between isolated habitat patches as a strategy for biodiversity conservation (Donald & Evans, 2006; Lees & Peres, 2008; P. Williams et al., 2005). Connectivity may be achieved by restoring natural or inserting man-made linear habitat networks or corridors (e.g. hedgerows) between isolated patches (Françoise Burel, 1996). Habitat corridors such as hedgerows aim to protect species that are expected to go extinct following habitat loss and fragmentation (Kuussaari et al., 2009). In **Chapter 4**, we studied whether hedgerows can act as potential corridors for forest plant species. Our hypothesis was formulated starting from the idea that most forest specialists are dispersal limited and their absence from recent hedgerows might be explained by the lack of

dispersal. In addition, we suggested that recent hedgerows might provide forest plant species with sub-optimal environmental conditions (e.g. high phosphorous content) that might impede germination success more than establishment success. This chapter represents an ongoing experiment. Once the full monitoring will be achieved, we will be able to answer the question whether the usual absence of forest specialists in recent hedgerows can be explained by dispersal and/or recruitment (germination or establishment) limitations. Furthermore, we will be able to conclude on the potential role of hedgerows in ensuring connectivity between isolated forest patches. Another feature of habitat corridors appears in **Chapter 2**, where one of the studied landscapes was forest patches connected by hedgerows within a matrix of grasslands (semi-fragmented forest patches or SF). Both forest generalists and specialists co-occured in this type of landscape although a less pronounced "community saturation" pattern of species richness might appear. Thus, the presence of hedgerows provides a form of connectivity between the forest patches and allows the coexistence of both generalists and forest specialists across the landscape.

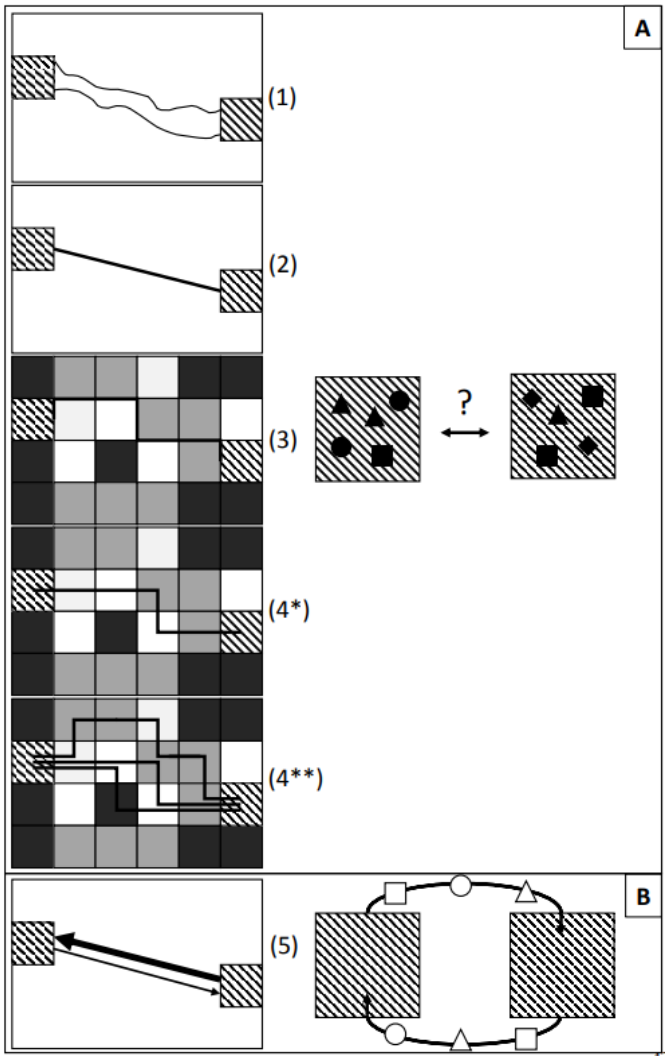

Figure 5-2: The influence of landscape connectivity on plant dispersal*. **(A)** Diagram depicting different potential dispersal regimes with different connectivity patterns. **(B)** This panel represents dispersal regimes with no observed connectivity between patches **(5)** but what is called "actual functional connectivity" due to high dispersal abilities. White squares having diagonal lines represent focal habitat patches. Squares, circles and triangles represent different plant species. **(1)** to **(4**)** represent different connectivity patterns (e.g. corridors in **(1)** and **(2)** and structural connectivity in **(3)**). Thick arrows in **(B)** represent higher dispersal rates while thin arrows represent lower dispersal rates. Extracted From Uroy, Ernoult, & Mony, (2019).*

The value of connectivity among habitat patches depends on whether species germination and persistence rates are controlled by species dispersal abilities relative to the configuration of the habitat patches within the landscape (Fig. 5-2) (Moilanen & Hanski, 1998). Species may show different response to connectivity, where highly mobile and vagile species

may not benefit from a connectivity increase (Bennett, 2003), while sessile organisms such as plant species are likely to benefit from connectivity as long as it falls within the dispersal range of a given species (Doerr & Barrett, 2011; Johst et al., 2011). With increased habitat fragmentation, the increased distance between habitat patches may exceed the dispersal capacity of species regardless of whether species are sessile or mobile (Dennis, Dapporto, Dover, & Shreeve, 2013). In addition, when considering the interaction between dispersal capacity and increased connectivity, we should also consider differences in dispersal mechanisms among species (Hodgson, Moilanen, Wintle, & Thomas, 2011). For example, plants dispersed by animals may benefit from increasing connectivity by the introduction of corridors that allow animals to move in or along the corridors, whereas wind-borne propagules might be blocked by corridors such as hedgerows(Brudvig, Damschen, Tewksbury, Haddad, & Levey, 2009).

5.4. Importance of species identity within plant community assembly

The role of dispersal and recruitment (germination and subsequent establishment) limitation has received growing attention with several studies recognizing their impact on community structure and composition (Stephen P. Hubbell, 2001; Verheyen & Hermy, 2001b). Though they are believed to play in a sequential manner with other processes, it is not a trivial approach to assess the respective effect of each of these processes (Ehrlén & Eriksson, 2000; Yu et al., 2004). Other processes may comply with these limitations and exert a profound impact on community dynamics. For example, the variability among species migration rates may be dependent on species capability to disperse, and the configuration of the ways by which this species will arrive to the new habitats. At the global scale, it is believed that not all species migrate at the same rate and other parameters such as species lifespan can affect their migration. Indeed, it has been noted that short-lived herbaceous plants are able to shift their elevational range faster than species with longer lifespans as climate warms (Lenoir, Gégout, Marquet, De

Ruffray, & Brisse, 2008), altering potential species interactions and consequently exerting a change in plant community composition (Lenoir et al., 2010).

Results from **Chapter 2** showed that species identity interferes in the sorting of species and their distribution when the focal habitat is fragmented. When studying the alpha-gamma relationship at different spatial scales and with three different fragmentation intensities, forest specialists exhibited a different behavior from generalists. In non-fragmented forests, habitat quality is considered adequate and dispersal is thought optimal, allowing forest specialists to persist and dominate. In the same non-fragmented habitat, generalists are believed to tolerate wider range of environmental conditions than specialists do, and to be associated with the forest gaps where conditions are sub-optimal for specialists. In highly fragmented forest habitats, dispersal limitation likely reduces the chance that specialists disperse and colonize forest patches. Moreover, edge effects in highly fragmented forests may further cause recruitment limitation for specialists (i.e. harsh habitat conditions and strong competition with generalists). Thus we must take into account the majority of abiotic conditions that affect species richness at the different levels of fragmentation. Our findings support several studies which showed that the variability among habitats appears to affect specialists more than generalists (Kolb & Diekmann, 2004; Pandit, Kolasa, & Cottenie, 2009). Vázquez & Simberloff, (2002) stated that the effect is higher on specialist species abundance when the focal habitat undergoes environmental alterations since generalists are able to utilize extensive range of habitat conditions. Thus, specialists are more prone to go extinct than generalists in case of any change in their habitat, and the increased levels of fragmentation and habitat loss should increase the concerns about the future dynamics of the respective share in generalist and specialist species (David Tilman, May, Lehman, & Nowak, 1994; Travis, 2003).

Another example of the importance of species identity appears when studying the weed community assembly in agricultural landscapes (**Chapter 3**). In this study, there were

differences in the abundance of weed species (annuals *vs.* perennials) according to the technical itineraries adopted. In the first place, both annual and perennial weed species appeared to be highly dispersal limited since the majority of the sown seeds succeeded in germinating. Annual weed species dominated in reduced tillage systems while perennials were more abundant in no-tillage systems and especially when incorporating a cover crop mix (leguminosae-Brassicaceae). Secondly, annual weed species were more affected by the field abiotic conditions: soil preparation (reduced tillage *vs*. no-tillage), while the majority of perennials were affected by biotic interactions: soil cover rotation (intercropping with CC-mix). These findings are consistent with former findings concerning both annual species abundance increase with reduced tillage while perennials are favored by no-tillage treatment associated with CC-mix (Bilalis, Efthimiadis, & Sidiras, 2001; Derr, 1994; Froud-Williams, Chancellor, & Drennan, 1984; M. W. Myers et al., 2005; A. G. Thomas, Derksen, Blackshaw, et al., 2004). In the same study, the allelopathic effect of *Camelina* intercrop appeared to be species-specific.

5.5. Importance of dispersal

Understanding the species-habitat relationships requires having knowledge about species vital rates (i.e. death, birth and dispersal), and the impact of environmental variables on their abundance (Zhang, Zhao, Zhao, & von Gadow, 2012). In the absence of experimentation, it is difficult to say with certainty whether species abundance is driven by either dispersal, biotic interactions or abiotic conditions. Therefore, overcoming dispersal by direct seeding of the studied species allowed us to test whether a certain species is either dispersal limited (i.e. germination success), or recruitment limited (no germination although seeds are present in the studied site). Dispersal is the most important ecological process that affect community assembly, colonization and biodiversity maintenance (Chase, 2003; Levine & Murrell, 2003; B. C. Wang & Smith, 2002).

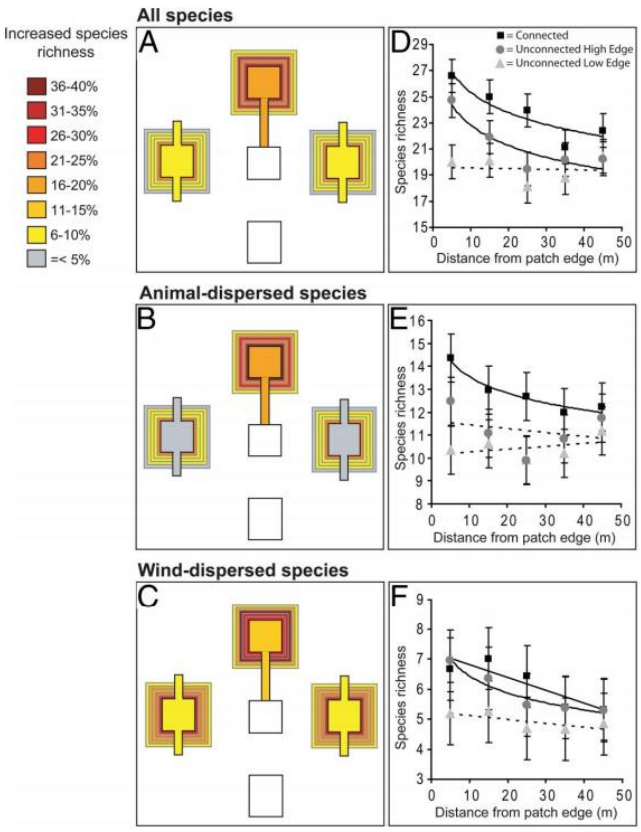

Figure 5-3: Species richness within different target patches and surrounding non-target habitat *showing different types of dispersal mechanisms. From (Lars A. Brudvig, Damschen, Tewksbury, Haddad, & Levey, 2009)*

The most advanced way to study dispersal limitation in local communities is to perform a seed addition experiment (Clark, Poulsen, Levey, & Osenberg, 2007; Myers & Harms, 2009; Zobel, Otsus, Liira, Moora, & Möls, 2000). These studies have showed an increase in biodiversity after propagule addition, which eventually reflects unsaturated communities. In order to understand which ecological processes (dispersal, competition and/or stochastic processes) alter local diversity, we may consider comparing the functional traits of the observed species with every studied process (e.g. overcome dispersal and study recruitment, or overcome both dispersal and abiotic limitations and study the effect of biotic interactions on germination and persistence). An example is the application of 'response-effect trait framework' (Zirbel, Bassett, Grman, & Brudvig, 2017) aiming to study the impact of environmental conditions in altering the plant functional traits; and the resulted changes in community assembly patterns

and ecosystem functioning. The extent to which dispersal limitation at macroecological scale may interfere in the plant species presence/absence is still poorly studied. Therefore, our study may increase the knowledge about the importance of dispersal in community assembly of plant populations. In **Chapter 2**, different dispersal patterns appear at the three studied fragmentation levels and for the two presented species types at different spatial scales (named scale factor in **Chapter 2**). The richness of generalists differs with spatial scale; this is explained by the wide range of dispersal capacities of these species allowing them to be abundant through the entire patch unlike forest specialists, for which establishment success in the forest core is chiefly controlled by habitat quality and biotic interactions. Forest specialist species usually have lower dispersal capacities (Kolb, Barsch, & Diekmann, 2006) allowing them to be more abundant at smaller spatial scales measures. When landscapes shift from non-fragmented to highly fragmented forests, forest plant specialists are more negatively affected due to their low dispersal abilities, while generalist herbs are more negatively affected by biotic and abiotic conditions. In **Chapters 3 and 4**, sowing the seeds directly in the field allows overcoming dispersal limitation, and therefore if species are retrieved after several monitoring, then we can conclude that dispersal limitation applies for this species. In **Chapter 3** (**Chapter 4** is still ongoing without valid results), several species appeared to be dispersal-limited such as: *Artemisia vulgaris, Plantago lanceolata, Coriandrum sativum, Centaurea cyanus* and *Echinochloa crus-galli*. Summing up our findings in the three previous chapters allows us to note that dispersal limitation is one of the main reasons that explain the presence or absence of certain plant species at a local site (Fig. 5-2 & 5-4). In addition, dispersal limitation appears to be less evident at smaller scales, which are more controlled by competitive interactions and abiotic conditions. These findings are consistent and in accordance with other previous experimental studies (Germain, Strauss, & Gilbert, 2017; Münzbergová, 2004; Pinto & MacDougall, 2010). Therefore, plant communities are controlled by dispersal limitation and

habitat availability at larger scales (Fig. 5-3), while environmental conditions and productivity may predict plant community patterns at smaller scales (Aavik & Helm, 2018).

5.6. Impact of competition

Species are unable to occupy the full range of conditions within their physiological space as long as competitors and other interacting species are present (Diekmann & Lawesson, 1999). As long as it affects plant fitness, the impact of competition significantly matters relative to the impact of other environmental conditions. Several studies have shown that the decreased in physical constraints (wide range of favourable environmental conditions) may result in increased plant biomass (Brooker et al., 2005; Brooker & Kikvidze, 2008; Gaucherand, Liancourt, & Lavorel, 2006; Pennings & Callaway, 1992). In comparing both the realized and the potential niches, the former being more restricted than the latter by the environmental variables, productivity and survival rates (G. Evelyn Hutchinson, 1957; Wasof et al., 2013). This difference allows species to be more or less ecologically restricted by the presence of other competing species (G. Evelyn Hutchinson, 1957). Despite that the difference between the potential and realized niche might be a result of biotic interactions is well adopted in ecology, the effect of biotic interactions on the niche difference between regions remains controversial with studies that are in accordance with this point of view (Diekmann & Lawesson, 1999) and others rejecting it (Manthey, Klicka, & Spellman, 2012). This refers to the hypothesis raised by McArthur, (1972) suggesting that niche width depends upon the size of the regional species pool: the more species in the regional pool, the stronger the competition with ecologically similar species, and thus the smaller the realized niche. Contrary to the hypothesis from McArthur, (1972), results in **Chapter 2** show that in non-fragmented forests (continuous and contiguous forests) species might be more affected by abiotic conditions than by competition. Both generalists and specialists might co-occur together with less competitive events and with generalists being distributed throughout the whole forest while specialists are mainly presented

in the forest core. However, in highly fragmented landscapes, competition between generalists and specialists may also be the main key player allowing generalists to dominate with decreased niche width and diversity for forest specialists.

Results from **Chapter 3** highlight the importance of competition in agro-ecological systems. We adopted the no-tillage system to assess the effect of biotic interactions (especially competition) between two different intercrops and weed community. Results from this study show that winter cover crop mix (leguminosae-Brassicaceae) suppresses the most dominant weed species (*Echinochloa crus-galli*), consistently with the diversity-complementarity hypothesis, since the latter species likely competes with other weed species for space, light and resources. In addition, future results from the study presented in **Chapter 4** may highlight the importance of competition in the assembly of forest specialists in hedgerows. In the studied transects (forest and hedgerows), each transect is divided into two different linear sides with different disturbance regimes. One of the sides is kept without disturbance (with vegetation) allowing to monitor the germination/persistence of the studies species (as seeds and/or transplants) and revealing the effect of biotic interactions (competition) on the presence of forest herbs in hedgerows.

Based on the outcome of the three previous chapters, biotic interactions seem to be less important than species local adaptation and local environmental variables. A general question of how the differences among species may influence the outcome of competition may arise and assist in explaining one of the central ecological debates that is the niche-neutral debate (Adler, HilleRisLambers, & Levine, 2007; J. J. Wiens, 2011). Indeed, answering this question requires the separated study of both niche and competitive ability differences, and several studies have attempted to explain these differences (Adler et al., 2007; Chesson, 2000b; Mathew A. Leibold & McPeek, 2006; Levine & HilleRisLambers, 2009). By quantifying the competitive trait values in various ecological systems (Navas & Violle, 2009), we will be able to identify the

differences between niche effect and competitive ability relative to these traits, and eventually have a clearer idea about the importance and role of competition in plant community assembly.

5.7. Environmental filtering vs. competitive exclusion

Theoretically, it is clear that in order to demonstrate environmental filtering we need to show that a species is able to arrive to the site but unable to tolerate the abiotic conditions of that site. In practice, however, the required data are difficult to obtain due to the challenge of disentangling species tolerance to the site conditions from biotic interactions. Studying the relative importance of these two processes contributes to the discussion of the difference between the potential and realized niche (Malanson, Westman, & Yan, 1992; McGill, Maurer, & Weiser, 2006). Mayfield & Levine, (2010) stated that both competitive differences and abiotic tolerance differences might result in phenotypic similarity among species within plant communities and especially that the phenotypic traits that are associated with these differences are unknown. Consistently, our results in **Chapter 2** did not provide clear evidence on whether habitat suitability or biotic interactions are responsible for the observed patterns in species diversity (coexistence of both forest specialists and generalists with forest specialists being favoured) within non-fragmented forests. Similarly, in highly fragmented forests, it is still uncertain whether harsh environmental conditions (generalists are more tolerant to environmental conditions than forest specialists) or stronger competition (generalists are stronger competitors than forest specialists) is the main driver of community assembly. However, other studies highlighted that it is possible to differentiate between phenotypic traits that are associated with competition from other traits that are associated with abiotic tolerance (Gaudet & Keddy, 1988; Godoy & Levine, 2014; D. E. Goldberg & Landa, 1991). Our findings in **Chapter 3** are consistent with results from these studies and may be further supported by the future findings of **Chapter 4** (which should allow us to distinguish between environmental filtering and competitive exclusion). Indeed, the experimental design of **Chapter 3** allowed us

to differentiate the effect of competition from the effect of abiotic condition on weed community assembly. For example, findings of this study highlight the effect of biotic interaction (the diversity-complementarity hypothesis) since the source of abiotic disturbance is absent (no-tillage) in some plots. However, keeping the soil without vegetation cover in both winter and summer allows studying the effect of abiotic disturbance of weed community, since the only key player in these plots was the soil disturbance (i.e. reduced tillage). Kraft et al., (2015) demonstrated this trait based distinction via two-step quantification, where the first step is assessing the survival of plant species in absence of neighbours; and thereby studying species environmental tolerance solely. The second step is quantifying persistence of plant species having biotic interactions with their surrounding species. It may be also important to quantify the correlations (positive and negative) resulting from species interactions. These correlations may exert some complications during the observation of phenotypic patterns, for example: species having traits associated with abiotic tolerance may result in trade-offs altering the co-occurring species growth and reproduction and eventually result in reduced competitive ability (Grime et al., 1997; Grime, 1977; Grime, 1997). On the other side, positive interactions with other species may increase the co-occurring species performance allowing them to persist in environmental conditions that they were not able to tolerate (Kraft et al., 2015).

5.8. Conclusions, implications and future perspectives

A large body of literature addressing the effects of dispersal and recruitment limitations tried to explain plant community patterns. Community assembly rules aim to account for the mechanisms structuring plant communities (Fig. 5-4). In addition, community assembly processes may answer one of the long-standing questions in ecology, that is of whether plant species, after successfully reaching a focal site, form communities due to the effect of interacting species, and thus show non-random patterns of assemblages (Clements, 1916) or

whether species are randomly distributed in the limit of their ability to tolerate similar environmental conditions (Gleason, 1926).

In this thesis, we investigated the role of dispersal and recruitment limitations in patterning vascular plant species assemblages in different types of landscapes. How can our findings contribute to further our understanding of metacommunity dynamics? Each of the chapters of this thesis demonstrated some general conclusions concerning plant community assembly and the importance of both dispersal and recruitment limitations. In **Chapter 2**, we highlighted the impact of forest fragmentation on herbaceous forest plant species distribution. Results from this chapter revealed the role of species identity (generalists *vs*. forest specialists) in explaining plant community patterns. Fragmentation altered the dispersal and recruitment abilities of plant species (both generalists and specialists) from one side, and caused a change in habitat quality (environmental conditions) from the other side. This change in the assembly of forest plant communities may explain the observed shifts in the alpha-gamma diversity relationship (AGR) from "proportional sampling" towards "community saturation". In **Chapter 3**, we examined the biotic and abiotic effects on the assembly of weed communities in agricultural crops. In the first place, nearly most species succeeded to germinate in the field thereby showing that they are dispersal limited. Recruitment of weed species was driven by both biotic and abiotic factors, with the presence of cover-crop mix exerting a form of biotic constraint (diversity complementarity), thereby suppressing the germination and persistence of weed species (in addition to the allelopathic effect of *Camelina*). Therefore, the presence of cover crop mix with no-tillage treatment was considered a win-win strategy by suppressing weed species from one side, and enhancing crop yield with less environmental damage from the other side. In **Chapter 4**, our preliminary results show that germination was the main limitation for forest plant species to occur in recent hedgerows rather than being limited by dispersal. In addition, seed viability may be another reason behind the lack of germination in

hedgerows since most of the studied species failed to germinate in the greenhouse experimentation. The age of both hedgerows and experimental forest may be considered to affect species germination where hedgerows are too recent and not mature enough in terms of the soil characteristics (e.g. soil moisture, phosphorous content) being far from a mature forest soil. The rather low germination rate found in the experimental forest could also be due to the fact that this forest is maybe rather too recent (since 1989) and thus the soil does not resemble a mature forest soil, which could partly explain the low germination rate. Future results from further surveys may provide a clear idea about the assembly of forest specialists in hedgerows being driven by either dispersal, recruitment, or persistence.

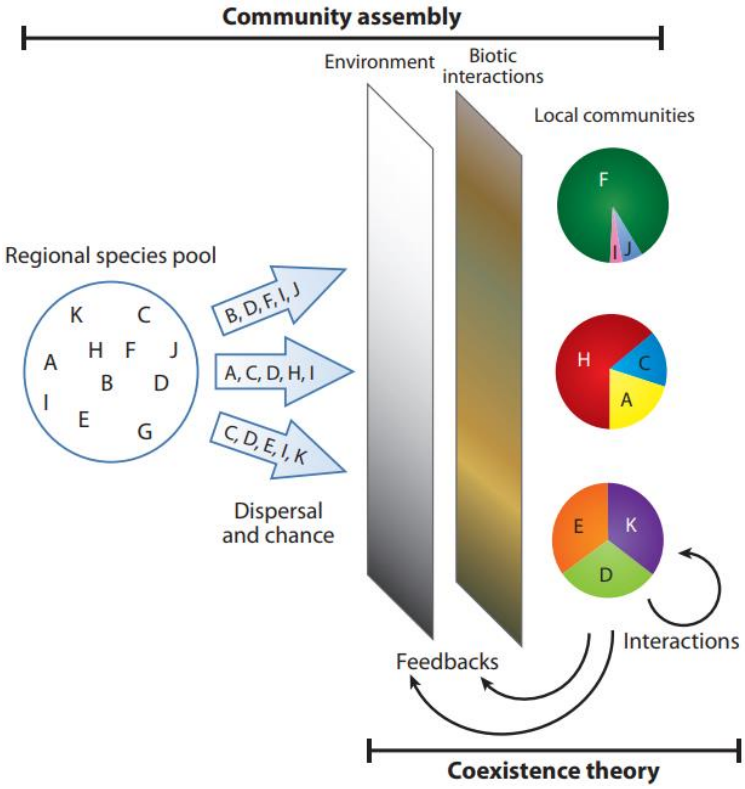

Figure 5-4: Community assembly is believed to be affected by different processes operating with a wide range of spatio-temporal scales*. Species inside the regional species pool are the result of different historical processes (e.g. speciation and evolution). Potential species that are ready for colonization will be affected by dispersal events before passing through biotic and abiotic filters in order to achieve the local or actual communities. All the mentioned post-dispersal processes, in addition to the local species interactions, are considered the main*

aspects for studying species abundance and coexistence. Extracted from (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012).

Therefore, there is a potential for more investigation in **Chapters 2, 3 & 4**. In **Chapter 2**, we may assess the dark diversity (i.e. species that should be present in the studied habitats but are currently absent) in the different patches and study the effect of the change in fragmentation level on the dark diversity of the herbaceous species. During the survey of **Chapter 3**, we collected the LAI (leaf area index) of the different 24 plots. The LAI may be used to assess the amount of light intercepted by the plant canopy and it may be a significant parameter for studying the crop growth. In addition, the study of **Chapter 3** paves the way for studying the germination and crop yield of the second cash crop (i.e. *Camelina*). In **Chapter 4**, there is a potential for replicating a similar design along a gradient of hedgerow and forest age, from very recent hedgerows and forests (current study) to very ancient hedgerows and forests. This would help to better understand whether recruitment limitations found in our results are mainly affected by the age of both hedgerows and forests or not. Addressing these mentioned potential studies may allow us to have a clearer understanding of the multitude of ways to explain the patterns of variation in plant community assembly (Fig. 5-4) and draw out robust implication for biodiversity conservation.

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ANNEXES

Appendix 2-1: Data table (raw data) used in the log-ratio model showing the species richness (forest specialists, generalists and total) as well as the value of several covariates at different spatial scales across the 116 studied forest patches.

plot_ID	ALL_1	ALL_10	ALL_100	ALL_1000	ALL_T	FS_1	FS_10	FS_100	FS_1000	FS_T
BB01	5	14	28	48	62	0	4	7	11	16
BB02	4	8	18	33	41	0	3	8	10	17
BB03a	4	5	5	8	13	0	0	0	1	1
BB03b	7	11	25	48	59	2	2	3	7	9
BB03c	9	15	29	36	51	1	4	8	10	16
BB06	2	5	8	12	17	0	0	0	0	0
BB10	3	4	6	11	15	0	0	1	1	2
BB20	6	8	10	26	34	0	1	2	4	5
BB24a	2	6	8	25	31	0	0	0	2	2
BB24b	10	14	22	38	52	1	2	5	6	8
BB33	3	3	6	10	13	0	0	0	2	2
BB33b	3	4	5	7	11	0	0	0	0	0
BB35	3	3	9	15	18	0	0	0	2	2
BB36	2	5	16	30	35	0	0	4	10	11
BB41	4	10	17	40	50	2	2	5	12	14
BC01a	8	12	19	29	41	3	4	6	8	9
BC01b	8	14	21	31	45	3	6	11	13	16
BC02	2	2	3	12	14	1	1	1	4	6
BC03	8	9	18	34	43	4	4	6	11	13
BC04a	6	10	19	38	48	3	6	8	14	17
BC04b	5	7	12	19	26	2	2	3	7	9
BC04c	6	14	21	33	47	0	2	4	6	7
BC05	5	13	22	36	49	0	0	5	9	11
BC06	7	14	23	44	58	2	5	9	17	19
BC06b	5	5	16	26	31	3	3	8	10	14
BC07	1	3	7	11	14	1	1	1	2	4
BC17	2	2	11	28	30	1	1	2	4	4
BC22	6	11	22	37	48	1	2	6	11	13
BC23	4	7	15	26	33	0	1	5	9	14
BC25	5	8	17	43	51	0	0	5	13	16
BT01	4	6	16	27	33	1	1	4	7	10
BT02	6	11	24	49	60	2	5	6	13	16
BT05	6	13	16	21	34	2	5	6	6	9

BT06	3	6	11	27	33	0	2	4	11	11
BT07	5	7	21	37	44	2	3	9	12	14
BT08	5	10	19	33	43	1	4	7	9	11
BT11	4	12	21	38	50	1	5	7	10	17
BT12	5	13	26	43	56	1	2	9	14	22
BT13	5	7	18	28	35	1	1	5	6	8
BT18	13	19	23	57	76	2	5	7	15	19
BT21	8	10	17	36	46	4	4	6	12	13
BT27	12	21	33	50	71	2	5	7	10	19
BT38	8	14	26	44	58	1	2	6	9	14
FB04	4	7	11	18	25	0	0	1	3	4
FB06	3	9	16	28	37	1	2	5	11	14
FB09	2	3	4	7	10	0	0	0	0	0
FB10	1	4	7	17	21	0	0	1	5	5
FB13	2	5	8	21	26	1	1	2	6	6
FB15	3	6	12	22	28	0	0	2	7	7
FB16	2	2	2	6	8	0	0	0	2	3
FB17	6	7	21	42	49	0	1	6	12	13
FB19	1	2	8	14	16	0	0	1	3	4
FC01	4	7	10	19	26	0	1	2	5	6
FC02	5	10	15	31	41	1	4	5	11	13
FC03	1	4	7	19	23	0	0	1	7	7
FC04	2	6	9	18	24	0	0	1	5	5
FC05	4	6	10	14	20	0	0	1	5	6
FC06	2	4	7	16	20	0	0	0	5	6
FC07	2	2	4	16	18	1	1	1	3	4
FC09	1	3	5	11	14	0	0	0	2	4
FC13	1	3	9	22	25	0	0	1	8	8
FC14	11	16	26	36	52	3	5	11	12	14
FC18	5	13	22	39	52	1	3	4	12	16
FC19	3	6	14	32	38	0	1	2	8	9
FC20	6	9	28	47	56	3	3	10	13	15
FC21	3	4	7	24	28	1	1	2	10	13
FC22	3	6	12	17	23	1	2	6	7	9
FT01	3	8	12	21	29	1	1	1	4	5
FT02	4	6	12	20	26	0	0	1	6	9
FT03	9	11	15	23	34	2	2	3	5	6
FT07	4	7	13	30	37	1	1	2	10	12
FT08	5	5	18	29	34	0	0	7	8	11
FT09	2	4	12	23	27	0	0	3	6	8
FT10	6	8	10	14	22	0	2	3	4	7
FT11	5	8	10	23	31	0	0	0	6	7
FT12	2	4	5	21	25	0	0	1	5	7
FT13	2	6	10	17	23	0	0	3	3	6
FT17	12	19	21	29	48	4	7	7	9	14

FT21	7	12	15	34	46	3	6	6	12	15
FT23	5	9	15	24	33	1	3	4	7	9
FT30	2	6	8	26	32	0	2	2	6	9
FT32	4	7	10	26	33	2	2	3	9	13
OB01	7	14	22	31	45	4	7	11	14	17
OB02	2	5	8	14	19	0	0	1	1	4
OB05	1	3	5	6	9	0	1	2	3	4
OB06	3	7	11	20	27	0	1	2	5	8
OB07	6	10	18	23	33	0	1	2	4	6
OB13	3	5	9	19	24	0	1	2	2	8
OB17	9	16	23	30	46	2	3	3	5	8
OB18	4	9	14	22	31	0	0	1	2	4
OB19	3	7	10	22	29	1	1	2	2	2
OB22	5	8	13	22	30	1	1	1	2	4
OB27	9	12	23	33	45	1	2	4	7	11
OC01	5	8	15	20	28	2	3	6	7	8
OC09	4	6	14	22	28	1	1	1	2	2
OC14	10	17	25	32	49	2	4	7	9	9
OC16	2	5	13	26	31	1	1	5	9	13
OC20	8	14	16	21	35	2	6	7	8	12
OC22	5	5	11	14	19	2	2	3	4	5
OC24	13	21	26	33	54	6	10	14	17	18
OC25	14	19	25	34	53	4	5	6	7	11
OC26	8	10	16	36	46	3	5	7	11	12
OC27	5	10	17	26	36	3	5	9	11	15
OC29	3	9	15	29	38	1	4	6	10	14
OC30	11	15	20	34	49	5	7	9	15	18
OT02	5	9	15	24	33	1	2	5	7	10
OT04	5	10	15	27	37	2	5	7	11	14
OT05	4	5	18	28	33	1	1	1	3	5
OT07	3	13	21	33	46	0	2	4	6	8
OT09	7	9	13	33	42	2	2	3	12	13
OT14	4	11	21	31	42	1	4	6	13	17
OT15	6	11	17	27	38	0	2	2	4	10
OT20	8	15	18	28	43	2	3	3	7	12
OT24	3	7	16	30	37	1	1	4	5	7
OT28	3	4	8	18	22	1	1	1	3	6
OT30	1	3	8	24	27	0	1	2	3	3

FG_1	FG_10	FG_100	FG_1000	FG_T	Shape_length	Area	Age	pH_1	C:N_1	P_1
1	3	8	17	21	936,108	23005,467	45,006	5,420	12,394	13,390
2	2	5	11	15	1670,460	70517,761	66,545	4,300	16,944	11,020
2	2	2	3	7	10402,811	622036,915	252,000	4,050	19,643	10,140
4	8	18	32	44	10402,811	622036,915	252,000	5,260	11,412	3,260
4	6	10	14	24	10402,811	622036,915	252,000	3,840	12,296	3,010
1	3	5	5	9	1005,764	54833,902	119,808	3,200	21,613	17,550
1	1	1	3	5	1957,018	85353,350	41,829	3,400	19,667	18,690
3	3	4	14	20	9715,498	397754,308	32,250	7,580	12,646	14,690
1	4	5	10	15	3778,748	274643,181	252,000	3,430	20,084	18,080
9	11	16	27	47	7222,085	592301,165	252,000	5,500	9,824	17,510
2	2	5	6	10	12623,214	1746113,714	160,957	3,860	12,375	21,090
2	3	3	4	9	12623,214	1746113,714	41,829	3,450	16,714	8,860
2	2	4	6	10	829,221	36655,646	144,595	2,920	18,412	6,810
1	1	6	10	12	1497,232	81176,142	54,892	3,120	11,242	2,640
2	2	4	17	21	4687,373	424813,875	137,105	4,530	12,091	2,830
3	4	5	8	15	3933,526	365017,007	41,829	5,270	21,167	8,670
2	4	5	11	17	3933,526	365017,007	45,006	3,620	19,419	15,410
1	1	1	2	4	1313,908	76549,823	155,129	3,260	12,384	5,600
1	1	3	10	12	2063,181	109677,372	84,470	4,470	19,704	3,790
0	1	3	6	7	3778,748	274643,181	47,912	3,920	9,670	5,660
1	1	1	2	4	6001,851	331934,282	54,892	3,230	13,345	27,660
1	2	4	9	12	6001,851	331934,282	45,634	6,740	22,929	11,060
1	3	5	13	17	696,651	16718,939	12,000	4,500	11,843	5,140

1	2	5	12	15	3778,748	274643,181	177,376	4,040	13,667	2,610
0	0	4	5	5	3778,748	274643,181	59,464	6,890	13,987	25,850
0	0	1	2	2	1660,166	96777,190	87,781	4,030	19,643	27,460
1	1	3	15	17	567,870	17301,729	96,558	3,870	15,967	2,490
2	4	8	11	17	573,831	11487,773	137,265	4,590	13,596	10,500
2	3	5	9	14	277,709	4801,068	59,026	4,700	11,600	64,550
1	1	2	18	20	1248,046	35904,882	59,464	3,350	17,300	6,930
0	0	2	4	6	573,717	15224,728	45,634	7,260	13,014	15,810
1	1	10	21	23	2606,511	110600,661	41,342	4,100	12,854	5,640
1	3	4	5	9	386,706	10200,180	32,590	5,140	13,736	19,430
1	1	1	6	8	3169,420	130438,822	100,090	4,780	13,286	6,580
0	0	6	16	16	689,143	22762,067	47,912	6,480	12,375	15,900
2	3	7	13	18	572,884	15957,608	50,226	5,260	12,615	9,270
2	4	9	15	21	581,820	22370,931	57,727	6,770	12,413	14,520
3	5	10	21	29	996,861	56159,120	111,907	5,360	13,118	7,280
2	3	6	11	16	1270,297	46951,232	58,534	4,390	12,632	6,900
5	7	9	29	41	548,077	18166,494	51,573	4,830	14,256	9,990
3	3	4	9	15	1596,532	41692,481	37,844	4,610	11,440	13,600
7	12	19	26	45	438,312	12541,463	45,938	4,420	12,982	14,040
3	6	12	23	32	403,045	9747,391	49,967	5,180	13,719	2,940
1	2	3	4	7	3819,003	457147,752	238,882	5,000	11,042	3,150
1	5	6	10	16	977,612	46743,984	252,000	4,280	12,677	5,290
1	2	3	3	6	1135,345	79681,908	202,609	6,210	14,893	19,330
1	2	2	5	8	1445,221	59124,950	237,237	4,670	14,000	13,510
1	1	1	7	9	779,599	34210,352	243,467	5,780	14,427	16,900
1	3	4	7	11	561,078	18780,887	225,115	5,020	13,233	16,230
1	1	1	2	4	674,647	24746,868	252,000	7,210	19,058	37,340

1	1	6	15	17	557,167	19046,229	252,000	3,480	14,400	10,790
1	1	1	2	4	451,539	12587,590	252,000	3,860	18,167	9,000
2	4	5	10	16	3027,523	558370,245	252,000	4,200	12,833	10,970
2	3	7	15	20	2681,349	378955,892	252,000	4,390	14,036	8,720
1	2	4	8	11	3833,931	332834,108	252,000	3,980	15,471	8,220
1	3	4	7	11	1850,049	121093,450	252,000	5,060	15,225	4,870
1	3	4	4	8	1855,421	94850,314	252,000	3,620	19,735	7,740
1	2	4	6	9	1512,364	83368,508	252,000	3,850	15,726	12,860
0	0	2	9	10	1217,043	69125,921	252,000	4,920	15,432	18,490
1	1	1	4	6	1809,242	54680,377	252,000	3,570	13,778	8,300
1	1	2	6	8	1015,430	44727,687	252,000	3,200	15,385	9,290
4	5	7	14	23	570,655	12950,390	194,000	4,240	19,800	3,520
2	7	15	21	30	345,776	6915,987	252,000	3,590	16,625	2,970
2	2	6	15	19	285,423	5079,420	252,000	3,890	14,179	8,040
2	3	13	25	30	309,888	5218,403	252,000	3,480	17,147	5,880
1	1	2	8	10	341,638	5927,069	252,000	3,820	13,931	7,760
1	3	4	6	10	268,493	3807,435	252,000	3,700	16,097	4,860
2	6	6	10	18	300,254	20726,633	252,000	3,880	14,188	13,870
3	4	6	8	15	3230,628	223048,843	252,000	4,100	15,722	5,610
4	4	7	11	19	2037,743	193153,566	252,000	4,850	14,636	10,720
1	2	5	12	15	1006,706	38147,170	252,000	3,190	16,167	7,780
3	3	7	13	19	757,919	34598,046	226,054	4,120	15,850	6,060
0	1	5	12	13	726,300	26291,064	252,000	4,030	14,000	3,550
4	4	5	8	16	761,941	20726,633	252,000	4,100	15,739	8,540
2	4	5	10	16	697,165	20492,058	252,000	3,840	13,778	4,640
2	3	3	13	18	675,697	19674,039	252,000	3,810	12,320	4,910
0	2	3	7	9	573,607	19189,096	194,000	3,980	14,186	3,530

5	7	8	13	25	511,553	13138,834	252,000	4,270	11,417	1,400
2	3	4	12	17	460,764	10711,811	194,000	3,230	14,344	5,050
1	3	4	8	12	486,264	9569,052	252,000	3,270	13,968	5,830
1	3	4	11	15	300,254	5513,042	252,000	4,000	13,357	12,240
1	3	4	9	13	405,256	4592,874	252,000	3,420	13,855	2,760
2	4	4	8	14	3458,579	415121,557	186,823	3,890	15,165	11,080
0	0	0	1	1	810,386	25418,578	110,093	3,820	16,435	2,250
0	0	1	1	1	1829,103	157564,244	190,522	3,640	14,440	2,600
0	0	1	5	5	674,825	28449,481	92,751	3,710	12,200	2,350
1	2	2	3	6	2164,625	108283,829	57,584	4,110	13,697	1,670
0	1	1	2	3	455,251	12907,311	71,847	4,190	14,281	2,010
2	4	6	7	13	1307,200	38412,656	59,919	3,710	12,125	2,720
1	3	6	7	11	507,328	14634,105	81,175	4,160	12,941	6,550
1	3	3	8	12	829,365	26516,134	67,590	7,520	18,429	16,640
0	1	2	5	6	790,905	20628,614	86,686	7,540	16,795	14,910
3	4	9	15	22	480,242	13705,981	130,974	6,770	15,279	23,140
1	2	4	5	8	1780,830	204807,565	135,239	4,320	16,688	6,450
0	0	4	5	5	488,064	14646,971	12,000	5,970	17,377	27,220
4	8	10	13	25	345,920	6588,603	42,722	3,690	17,167	32,950
1	3	3	7	11	5428,056	601684,489	124,049	3,500	13,241	18,220
3	4	5	6	13	1686,846	74640,520	51,997	7,940	18,050	13,320
1	1	3	2	4	971,612	35255,846	59,787	5,550	13,545	4,100
5	6	6	8	19	1864,193	35255,846	37,144	6,510	32,591	13,050
5	7	9	12	24	1163,305	43044,695	53,398	5,900	19,841	22,320
1	1	3	10	12	1264,017	32656,312	56,391	5,820	13,886	12,370
1	1	2	5	7	2528,279	131643,546	129,885	6,190	14,583	18,740
0	1	2	6	7	887,119	41780,629	43,541	5,640	12,627	10,940

3	4	4	9	16	1848,231	141730,653	99,023	3,500	13,400	1,270
3	5	7	12	20	938,547	23879,401	12,000	6,110	16,851	12,930
3	4	5	11	18	2514,068	217895,649	162,541	6,040	20,216	16,350
0	1	5	7	8	674,371	27255,856	51,730	5,600	12,393	4,070
1	2	2	4	7	1634,487	64491,096	58,002	4,260	15,875	4,530
2	3	4	13	18	1463,382	45647,826	56,817	7,640	22,628	52,270
1	5	8	10	16	1933,382	130973,601	124,258	7,780	17,442	9,690
3	3	3	3	9	1624,114	51565,242	55,613	5,940	22,696	8,770
4	6	8	9	19	1989,367	76424,603	153,895	7,730	21,186	19,340
0	0	2	7	8	1100,139	40231,507	133,625	3,620	12,118	10,330
0	1	3	5	7	1293,276	33820,271	120,930	6,200	11,681	19,790
0	0	1	5	7	770,894	25627,179	54,734	5,950	20,942	23,120

Prop_forest_1	pH_10	C:N_10	P_10	SCA_10	Prop_forest_10	pH_100	C:N_100	P_100	SCA_100
2,930	5,710	13,414	11,210	3	2,930	5,783	13,208	10,893	3,6
8,981	4,115	15,026	9,335	0	8,981	4,213	14,482	9,370	2,0
35,755	3,775	18,311	17,225	2	35,755	3,700	17,970	14,667	2,0
52,889	5,640	11,464	4,335	3	52,889	5,740	11,241	13,010	2,8
37,101	3,770	12,187	3,455	3	37,101	3,817	12,312	4,913	2,4
29,361	3,240	23,980	14,040	2	29,361	3,243	23,131	16,580	2,0
23,458	3,290	19,567	21,005	5	23,458	3,297	19,725	17,950	3,1
28,009	7,615	12,962	14,430	0	28,009	7,583	13,786	15,087	5,0
56,700	3,350	19,020	16,295	0	56,700	3,287	19,229	12,420	2,2
41,828	5,395	9,131	45,590	0	41,828	5,300	9,077	33,773	3,0
97,072	3,765	13,320	14,445	0	97,072	3,740	13,081	16,577	1,7
83,535	3,450	14,641	6,425	0	83,535	3,443	14,068	9,200	2,5
16,033	2,960	17,942	5,425	2	16,033	2,990	17,658	13,767	3,0
28,742	3,165	11,294	3,735	0	28,742	3,353	11,030	4,607	2,4
86,371	4,575	12,022	3,695	3	86,371	4,677	12,069	6,897	2,7
30,083	5,150	23,379	7,645	4	30,083	5,273	22,624	7,637	3,8
27,835	3,395	19,231	13,335	0	27,835	3,460	19,384	9,673	3,3
12,602	3,330	12,787	5,525	0	12,602	3,300	13,606	5,460	2,0
16,844	4,500	18,644	4,790	0	16,844	4,373	18,886	5,203	3,4
41,593	4,180	8,984	6,765	5	41,593	4,147	8,934	6,053	3,8
29,747	3,185	13,339	16,755	1	29,747	3,250	13,872	13,103	2,8
40,508	6,780	22,336	11,010	0	40,508	6,840	19,976	12,157	3,6
3,975	4,040	11,181	5,275	3	3,975	3,953	11,272	5,490	3,6
44,433	3,765	14,333	9,785	0	44,433	3,730	14,259	8,940	3,8
26,348	7,020	14,127	25,460	0	26,348	6,980	13,630	21,500	3,0
38,023	3,860	20,551	18,675	4	38,023	4,643	19,981	13,443	4,5
14,438	3,955	15,857	5,780	3	14,438	3,937	15,728	4,910	4,4
7,179	5,010	13,129	10,640	0	7,179	5,287	12,957	10,373	3,0
6,386	4,660	11,718	70,255	2	6,386	4,693	11,573	74,607	2,8
7,556	3,335	17,127	3,770	5	7,556	3,453	16,341	3,330	4,2
31,369	7,110	13,055	14,340	5	31,369	7,077	13,406	15,300	3,4
26,844	4,105	13,181	6,065	5	26,844	4,127	13,417	5,977	5,0
5,699	5,135	13,135	16,720	2	5,699	5,123	13,084	16,063	3,8
15,519	4,785	13,597	6,475	0	15,519	4,783	13,475	6,053	4,8
7,313	6,600	12,438	16,595	0	7,313	6,623	12,259	20,457	2,7
8,204	5,500	12,304	11,115	5	8,204	5,317	11,989	9,420	4,4
41,550	6,855	12,276	13,980	5	41,550	7,147	12,389	14,170	5,0
39,336	5,780	14,333	8,435	4	39,336	5,447	14,065	8,290	5,0
11,222	4,245	13,152	10,340	1	11,222	4,193	13,571	11,050	2,7
11,180	4,495	14,653	8,870	0	11,180	4,483	14,956	9,690	4,0
7,993	4,755	11,792	20,415	0	7,993	4,790	11,950	21,150	4,7
2,885	4,345	12,920	27,040	5	2,885	4,230	13,104	28,543	4,7
7,176	4,635	13,400	4,890	0	7,176	4,403	12,986	6,437	4,0
4,585	5,160	11,130	2,875	0	4,585	5,217	11,304	7,770	3,0

2,390	4,290	12,417	5,240	0	2,390	4,240	11,810	4,690	3,0
64,889	6,390	14,292	15,705	4	64,889	6,447	14,188	12,567	3,8
100,000	4,305	13,621	11,445	0	100,000	4,080	14,143	17,327	3,8
100,000	5,975	15,194	20,570	0	100,000	6,067	4,045	18,203	3,9
100,000	5,095	13,119	16,720	0	100,000	5,030	13,104	15,513	5,0
100,000	7,400	21,409	30,905	4	100,000	7,417	21,511	27,947	4,0
97,745	3,640	14,750	10,620	5	97,745	3,727	14,814	9,673	5,0
91,869	3,840	18,135	9,380	3	91,869	3,837	18,061	7,980	3,6
85,710	4,235	12,707	7,455	0	85,710	4,200	13,123	7,293	4,7
87,986	4,350	15,113	9,195	0	87,986	4,330	16,425	16,487	4,4
98,621	4,135	13,948	10,270	0	98,621	4,060	14,630	11,777	4,7
86,379	4,695	15,703	4,740	0	86,379	4,477	15,181	4,273	3,6
100,000	3,745	18,212	6,360	0	100,000	3,880	18,262	7,350	4,0
88,842	3,700	16,071	12,305	0	88,842	3,767	15,875	10,967	3,8
94,634	4,580	14,780	13,690	0	94,634	4,617	14,654	13,070	4,3
100,000	3,580	13,782	9,665	0	100,000	3,580	13,914	10,103	5,0
100,000	3,190	15,154	7,655	0	100,000	3,113	15,505	11,337	5,0
100,000	4,300	18,233	4,430	0	100,000	4,237	16,939	4,147	5,0
100,000	3,550	16,526	3,015	0	100,000	3,493	16,094	3,057	4,7
100,000	3,690	14,642	7,650	5	100,000	3,533	14,988	8,750	5,0
100,000	3,500	15,708	6,260	0	100,000	3,483	16,376	10,010	3,9
100,000	3,695	14,712	6,015	2	100,000	3,727	14,425	5,463	2,7
100,000	3,730	16,441	6,290	0	100,000	3,717	16,864	6,903	5,0
95,385	3,915	14,838	12,140	5	95,385	3,877	15,127	12,350	5,0
100,000	4,065	15,432	5,685	5	100,000	4,137	15,672	6,117	5,0
94,084	4,435	14,636	11,525	0	94,084	4,463	14,313	12,337	4,8
100,000	3,165	16,405	5,385	0	100,000	3,190	16,034	4,923	5,0
99,406	4,135	16,429	5,740	5	99,406	4,023	16,131	5,230	3,4
100,000	4,085	14,429	3,290	0	100,000	4,103	14,405	3,983	3,0
100,000	4,025	14,383	8,955	0	100,000	4,080	14,318	10,020	3,9
97,074	3,805	13,344	4,100	0	97,074	3,710	13,827	4,543	5,0
98,757	3,635	12,679	4,415	0	98,757	3,537	13,306	3,450	1,7
87,141	3,800	14,654	5,190	1	87,141	3,773	14,500	3,883	2,7
100,000	4,330	11,787	2,280	0	100,000	4,340	11,985	2,147	3,1
90,879	3,195	14,535	4,785	4	90,879	3,213	14,119	4,260	3,8
100,000	3,190	14,306	3,850	0	100,000	3,243	14,027	3,197	4,0
100,000	3,800	14,179	14,910	4	100,000	3,633	13,880	11,343	4,1
100,000	3,480	14,058	3,650	3	100,000	3,483	14,019	3,260	3,3
100,000	3,810	14,620	10,845	0	100,000	3,873	14,357	15,917	4,0
73,478	3,890	15,640	2,800	0	73,478	3,847	15,430	3,417	3,5
100,000	3,575	14,255	2,065	4	100,000	3,560	14,235	2,300	4,2
99,701	3,685	11,977	3,930	0	99,701	3,713	12,378	4,927	2,0
100,000	4,050	13,548	2,045	2	100,000	4,050	13,967	2,237	3,6
100,000	4,090	14,050	2,285	0	100,000	4,053	14,370	2,503	3,2
100,000	3,805	12,406	2,810	0	100,000	3,850	12,532	3,207	2,8

48,549	4,275	12,543	7,180	0	48,549	4,770	13,068	9,860	0,0
4,580	7,645	18,056	14,870	0	4,580	7,630	18,286	15,190	4,5
24,854	7,625	19,250	14,665	1	24,854	6,527	18,748	11,683	3,3
23,450	6,765	15,289	20,820	0	23,450	6,740	14,886	19,527	3,8
52,718	4,010	16,785	5,870	0	52,718	3,850	17,815	5,827	3,8
33,165	6,175	17,274	19,640	0	33,165	6,393	16,944	18,223	1,6
20,067	3,760	16,979	29,095	5	20,067	3,810	16,625	29,810	3,2
12,010	3,575	13,509	14,585	0	12,010	3,503	13,699	10,127	3,8
20,969	7,895	18,244	12,780	5	20,969	7,823	18,091	15,247	4,2
1,781	5,850	13,439	9,900	2	1,781	5,903	13,569	11,340	3,5
13,983	6,645	30,551	14,895	2	13,983	6,703	25,845	18,427	2,4
7,458	6,115	19,053	23,145	4	7,458	6,327	18,451	23,270	3,1
3,990	5,930	14,940	14,980	3	3,990	6,040	15,660	16,340	3,3
4,204	6,330	16,052	17,600	0	4,204	6,450	18,737	15,710	2,6
1,746	5,640	13,188	9,425	2	1,746	5,470	13,416	11,177	3,6
26,165	3,490	13,357	2,025	2	26,165	3,420	13,786	4,027	2,0
82,647	6,335	17,258	14,535	0	82,647	6,463	18,381	13,733	3,2
5,289	6,175	20,887	24,205	0	5,289	6,253	21,098	20,000	3,2
0,839	5,485	11,442	5,170	0	0,839	5,610	11,264	5,970	3,1
62,793	4,305	15,524	5,385	3	62,793	4,383	14,476	5,557	3,6
12,122	7,645	21,913	36,780	0	12,122	7,653	21,620	30,777	0,0
7,038	7,775	16,796	9,430	4	7,038	7,767	16,503	9,833	4,0
12,925	6,120	22,830	9,780	4	12,925	6,250	23,219	9,127	3,9
13,667	7,805	22,514	19,190	0	13,667	7,793	21,988	19,160	3,7
13,339	3,550	12,243	9,295	5	13,339	3,673	12,364	8,710	5,0
6,408	6,295	12,479	21,065	5	6,408	6,347	12,264	20,140	4,5
9,236	6,145	21,806	23,300	3	9,236	6,323	22,425	22,290	3,2

pH_1000	C:N_1000	P_1000	SCA_1000	Prop_forest_1000	Region	Window	FL
5,480	13,229	10,513	2,760	2,930	B	BB	SF
4,355	14,329	8,658	2,670	8,981	B	BB	SF
3,650	18,221	13,298	1,947	35,755	B	BB	SF
5,813	11,750	18,298	2,833	52,889	B	BB	SF
3,758	12,293	4,405	2,491	37,101	B	BB	SF
3,250	22,576	22,858	1,625	29,361	B	BB	SF
3,320	19,429	18,810	3,375	23,458	B	BB	SF
7,615	14,462	15,523	3,375	28,009	B	BB	SF
3,333	19,047	10,193	1,749	56,700	B	BB	SF
5,258	9,340	29,283	2,974	41,828	B	BB	SF
3,745	13,142	15,963	1,781	97,072	B	BB	SF
3,408	13,974	11,378	2,269	83,535	B	BB	SF
2,993	17,805	13,063	2,470	16,033	B	BB	SF
3,518	11,536	4,958	2,004	28,742	B	BB	SF
4,830	12,152	7,528	2,602	86,371	B	BB	SF
5,320	22,103	8,815	3,367	30,083	C	BC	SF
3,655	19,162	7,860	3,434	27,835	C	BC	SF
3,450	14,265	5,690	4,293	12,602	C	BC	SF
4,345	18,699	5,185	3,160	16,844	C	BC	SF
4,180	9,198	6,198	2,888	41,593	C	BC	SF
3,313	13,991	10,475	2,747	29,747	C	BC	SF
6,855	20,155	13,033	3,622	40,508	C	BC	SF
3,990	11,000	4,968	2,951	3,975	C	BC	SF
3,800	14,119	7,488	4,110	44,433	C	BC	SF
6,658	13,476	17,598	4,310	26,348	C	BC	SF
4,548	19,385	11,230	4,089	38,023	C	BC	SF
4,640	15,351	4,910	4,019	14,438	C	BC	SF
5,260	12,914	10,288	2,866	7,179	C	BC	SF
4,943	11,245	84,635	2,990	6,386	C	BC	SF
3,548	15,841	4,635	3,329	7,556	C	BC	SF
6,925	13,249	13,938	3,449	31,369	T	BT	SF
4,188	13,556	6,373	3,603	26,844	T	BT	SF
5,228	13,132	15,883	3,073	5,699	T	BT	SF
5,078	13,317	8,260	3,748	15,519	T	BT	SF
6,418	12,131	18,648	2,766	7,313	T	BT	SF
5,475	11,932	15,035	4,186	8,204	T	BT	SF
7,323	14,509	14,808	4,505	41,550	T	BT	SF
5,153	13,729	7,448	3,933	39,336	T	BT	SF
4,118	13,765	12,630	3,097	11,222	T	BT	SF
4,390	14,829	10,628	3,181	11,180	T	BT	SF
4,953	12,041	20,690	4,155	7,993	T	BT	SF
4,360	12,899	23,975	3,295	2,885	T	BT	SF
4,298	12,967	7,423	4,471	7,176	T	BT	SF
5,338	11,479	7,088	3,578	85,710	B	FB	NF

4,430	11,892	7,658	3,482	98,621	B	FB	NF
6,393	14,255	10,398	3,967	95,385	B	FB	NF
4,018	14,328	15,443	4,000	100	B	FB	NF
6,100	4,782	15,533	3,985	100	B	FB	NF
5,208	12,824	15,628	3,561	100	B	FB	NF
7,295	20,627	24,505	4,140	100	B	FB	NF
3,680	15,051	8,423	3,889	97,745	B	FB	NF
3,895	17,711	8,415	3,422	91,869	B	FB	NF
4,155	13,739	7,343	3,987	85,710	C	FC	NF
4,213	16,294	13,405	3,841	87,986	C	FC	NF
4,010	14,949	12,083	4,206	98,621	C	FC	NF
4,435	15,252	3,880	3,886	86,379	C	FC	NF
3,845	18,628	8,108	3,679	100,000	C	FC	NF
3,733	16,086	11,100	3,741	88,842	C	FC	NF
4,530	14,337	11,905	3,769	94,634	C	FC	NF
3,575	15,221	9,598	4,333	100	C	FC	NF
3,088	16,145	11,485	4,276	100	C	FC	NF
4,215	16,723	4,305	4,118	100	C	FC	NF
3,523	15,889	4,093	4,425	100	C	FC	NF
3,505	15,324	7,873	3,596	100	C	FC	NF
3,475	16,013	10,285	3,743	100	C	FC	NF
3,713	14,717	5,860	3,404	100	C	FC	NF
3,763	16,701	7,890	5,000	100	C	FC	NF
3,863	15,438	14,130	4,164	95,385	T	FT	NF
4,095	15,548	6,535	4,151	100	T	FT	NF
4,373	14,341	11,763	4,823	94,084	T	FT	NF
3,210	15,852	4,698	5,000	100	T	FT	NF
3,998	16,106	5,580	4,389	99,406	T	FT	NF
4,108	14,883	3,930	3,181	100	T	FT	NF
4,058	14,683	10,143	3,846	100	T	FT	NF
3,678	14,577	5,178	4,450	97,074	T	FT	NF
3,553	13,252	2,985	2,368	98,757	T	FT	NF
3,783	14,455	3,690	2,667	87,141	T	FT	NF
4,345	12,255	2,678	3,096	100	T	FT	NF
3,218	13,993	4,103	1,995	90,879	T	FT	NF
3,255	13,885	3,605	3,370	6,847	T	FT	NF
3,588	13,792	9,353	3,294	4,204	T	FT	NF
3,500	14,054	3,473	3,524	14,540	T	FT	NF
3,848	14,768	14,685	3,436	8,684	B	OB	HF
3,850	15,183	3,138	3,278	13,678	B	OB	HF
3,540	13,795	2,568	3,245	16,525	B	OB	HF
3,680	12,235	4,518	2,197	9,748	B	OB	HF
3,983	14,367	2,170	3,361	1,746	B	OB	HF
4,103	14,126	3,358	2,818	13,339	B	OB	HF
3,885	12,500	3,120	3,254	5,289	B	OB	HF

4,695	13,089	8,945	2,342	12,152	B	OB	HF
7,655	18,382	14,413	4,186	4,580	B	OB	HF
5,785	19,272	9,493	3,358	24,854	B	OB	HF
6,745	14,725	18,165	3,096	23,450	B	OB	HF
3,853	17,354	6,820	3,679	5,254	C	OC	HF
6,505	17,061	17,135	3,512	33,165	C	OC	HF
3,900	15,725	25,918	2,787	20,067	C	OC	HF
3,643	13,256	8,280	4,244	12,010	C	OC	HF
7,818	17,587	14,748	3,115	20,969	C	OC	HF
6,010	13,961	10,850	3,330	1,781	C	OC	HF
6,765	24,821	18,388	2,653	13,983	C	OC	HF
6,395	17,531	24,423	4,052	7,458	C	OC	HF
6,143	16,577	15,930	3,145	3,990	C	OC	HF
6,538	18,293	15,658	3,124	4,204	C	OC	HF
5,340	13,394	10,853	3,450	1,746	C	OC	HF
3,385	13,786	3,278	2,000	26,165	C	OC	HF
6,505	18,461	14,695	3,675	16,365	T	OT	HF
6,365	21,363	18,488	3,013	5,289	T	OT	HF
5,705	11,233	5,680	3,509	0,839	T	OT	HF
4,358	14,324	6,053	3,837	6,235	T	OT	HF
7,688	21,374	28,868	3,528	12,122	T	OT	HF
7,780	17,104	10,090	3,717	7,038	T	OT	HF
6,308	22,184	15,210	4,215	12,925	T	OT	HF
7,765	21,039	19,485	3,682	13,667	T	OT	HF
4,280	12,495	11,183	4,386	13,339	T	OT	HF
6,423	12,645	20,378	3,740	6,408	T	OT	HF
6,453	23,553	21,875	3,132	9,236	T	OT	HF

Appendix 2-2: Species list

List of herbaceous forest plant species occurring across the entire study area and classified as either forest specialists (FS) or generalists (FG) in addition to the total number of forest patches out of the 135 studied forest patches in which the focal species was found. *Source of classification: Oberdorfer (1957), Plant Sociology.*

Species name	Specialization	Number of patch in which it occurs
Adoxa moschatellina	FS	38
Aegopodium podagraria	FG	3
Agrostis canina	FG	1
Agrostis capillaris	FG	1
Agrostis stolonifera	FG	9
Ajuga reptans	FG	22
Alliaria petiolata	FG	9
Allium ursinum	FS	2
Anemone nemorosa	FS	47
Angelica sylvestris	FG	1
Anthoxanthum odoratum	FG	2
Anthriscus sylvestris	FG	6
Arctium lappa	FG	1
Arctium nemorosum	FG	3
Arrhenatherum elatius	FG	1
Arum maculatum	FS	83
Asplenium scolopendrium	FS	1
Athyrium filix-femina	FG	41
Blechnum spicant	FG	2
Brachypodium sylvaticum	FS	40
Bromus ramosus	FG	1
Calamagrostis epigejos	FG	1
Callitriche stagnalis	FG	1
Caltha palustris	FG	1
Calystegia sepium	FG	1
Campanula trachelium	FG	2
Cardamine amara	FG	2
Cardamine hirsuta	FG	1
Cardamine pratensis	FG	10
Carex acutiformis	FG	1
Carex flacca	FG	7
Carex pallescens	FG	6
Carex paniculata	FG	1
Carex pendula	FG	4
Carex pilulifera	FS	19

Carex remota	FG	22
Carex riparia	FG	2
Carex spicata agg.	FG	1
Carex strigosa	FG	1
Carex sylvatica	FS	85
Chaerophyllum temulum	FG	3
Chrysosplenium alternifolium	FG	1
Chrysosplenium oppositifolium	FG	1
Circaea lutetiana	FG	54
Cirsium oleraceum	FG	1
Cirsium palustre	FG	4
Convallaria majalis	FS	4
Cynosurus cristatus	FG	1
Dactylis glomerata	FG	5
Dactylorhiza maculata	FG	1
Deschampsia cespitosa	FG	45
Deschampsia flexuosa	FG	7
Digitalis purpurea	FS	3
Dryopteris affinis	FS	2
Dryopteris affinis	FS	1
Dryopteris carthusiana	FG	63
Dryopteris dilatata	FG	47
Dryopteris filix-mas	FS	74
Elymus caninus	FS	1
Elymus sp	FG	1
Epilobium hirsutum	FG	1
Epilobium montanum	FG	7
Epilobium parviflorum	FG	1
Epilobium sp	FG	1
Epilobium tetragonum	FG	1
Epipactis helleborine	FG	4
Equisetum fluviatile	FG	1
Eupatorium cannabinum	FG	3
Euphorbia amygdaloides	FS	34
Festuca gigantea	FG	9
Festuca lemanii	FG	1
Filipendula ulmaria	FG	6
Fragaria vesca	FG	22
Galanthus nivalis	FG	1
Galeopsis tetrahit	FG	28
Galium aparine	FG	67
Galium odoratum	FS	25
Galium palustre	FG	1
Geranium robertianum	FG	37
Geum urbanum	FG	79

Glechoma hederacea	FG	33
Glyceria fluitans	FG	4
Helleborus viridis	FS	1
Heracleum sphondylium	FG	9
Holcus lanatus	FG	7
Holcus mollis	FG	28
Hyacinthoides non-scripta	FS	42
Hypericum hirsutum	FG	5
Hypericum perforatum	FG	4
Hypericum pulchrum	FS	11
Inula conyzae	FG	1
Iris pseudacorus	FG	2
Juncus conglomeratus	FG	11
Juncus effusus	FG	25
Lamium galeobdolon	FS	66
Lapsana communis	FG	4
Listera ovata	FG	21
Luzula forsteri	FS	4
Luzula multiflora	FG	2
Luzula pilosa	FS	38
Lysimachia nemorum	FG	8
Lysimachia vulgaris	FG	1
Lythrum salicaria	FG	1
Melampyrum pratense	FG	1
Melica uniflora	FS	25
Mercurialis perennis	FS	29
Milium effusum	FS	69
Moehringia trinervia	FS	15
Molinia caerulea	FG	5
Myosotis scorpioides	FG	1
Narcissus pseudonarcissus	FG	1
Neottia nidus-avis	FS	3
Ophrys insectifera	FG	3
Orchis purpurea	FG	15
Origanum vulgare	FG	2
Ornithogalum umbellatum	FG	1
Osmunda regalis	FG	1
Oxalis acetosella	FS	25
Paris quadrifolia	FS	18
Persicaria hydropiper	FG	3
Phragmites australis	FG	1
Phyteuma nigrum	FG	1
Platanthera bifolia	FG	3
Platanthera chlorantha	FG	2
Poa nemoralis	FS	9

Poa pratensis	FG	1
Poa trivialis	FG	39
Polygonatum multiflorum	FS	56
Potentilla reptans	FG	1
Potentilla sterilis	FG	19
Primula elatior	FS	25
Primula veris	FG	9
Prunella vulgaris	FG	2
Pteridium aquilinum	FG	32
Ranunculus auricomus	FG	14
Ranunculus ficaria	FG	17
Ranunculus repens	FG	5
Rubus fructicosus agg.	FG	109
Rubus idaeus	FG	13
Rumex acetosa	FG	4
Rumex acetosella	FG	1
Rumex obtusifolius	FG	6
Rumex sanguineus	FG	7
Sanicula europaea	FS	6
Scrophularia auriculata	FG	1
Scrophularia nodosa	FG	22
Senecio ovatus	FS	12
Silene dioica	FG	11
Solanum dulcamara	FG	9
Solidago virgaurea	FG	1
Sonchus asper	FG	1
Sonchus oleraceus	FG	1
Stachys alpina	FS	1
Stachys sylvatica	FS	29
Stellaria alsine	FG	1
Stellaria holostea	FS	25
Tamus communis	FS	5
Taraxacum officinale agg.	FG	17
Teucrium scorodonia	FS	6
Torilis japonica	FG	1
Urtica dioica	FG	41
Vaccinium myrtillus	FG	1
Valeriana repens	FG	7
Veronica chamaedrys	FG	4
Veronica hederifolia	FG	5
Veronica montana	FG	19
Veronica officinalis	FG	8
Vicia sepium	FG	6
Vinca minor	FS	9
Vincetoxicum hirundinaria	FS	1

Viola hirta	FG	4
Viola odorata	FG	3
Viola reichenbachiana	FS	54
Viola riviniana	FS	5

Appendix 2-3: Description of the covariates used in the log-ratio models

Patch area and patch length were calculated using digitized forest patches in each window (based on recent aerial photographs, all taken after the year 2000). For calculating forest patch historical age, we reconstructed the historical changes in forest cover within the nine studied landscape windows using maps from the 18th, 19th and 20th centuries. From these maps, all forest patches were digitized, and patch historical age was estimated using the date of the oldest map on which a patch was already a forest. As a given patch may contain a mosaic of fragments with different historical ages, we calculated an area-weighted average of the historical age of all fragments composing a given patch.

Habitat quality within a focal forest patch highly depends on soil and light conditions. Within each of the 135 quadrats of $1000m^2$, soil samples from the 0-10cm horizon, were collected after litter removal along the diagonal containing the three nested sub-quadrats, i.e. at 0, 2.25, 7.1, and 22.4m from a corner taken at random, so that a total of 1, 2, 3 and 4 soil samples were available for the 1, 10, 100, and $1000m^2$ quadrats, respectively. At the lab, each soil sample was dried, sieved and analysed for organic matter content, total nitrogen (N), available phosphorus (Olsen P) and pH_{water} following AFNOR French norms (X31-109, X31-111, X31-113 and X31-104, respectively). Across all quadrats, soil pH, carbon-nitrogen ratio (C:N) and available P ranges from 2.92 to 7.94 (mean ± standard error: 4.90 ± 1.33), 9.67 to 32.59 (mean ± standard error: 15.12 ± 3.49) and 2.17 to 84.64 mg Olsen-$P.kg^{-1}$ (mean ± standard error: 12.30 ± 8.90), respectively.

Light availability within the herb layer level was estimated by calculating the community weighted mean values of the shade casting ability index (SCA) of the canopy species for each individual quadrat or sub-quadrat based on the SCA index of each individual species weighted by its abundance within the quadrat or sub-quadrat (Verheyen et al., 2012). The SCA index is

an expert-based, species-specific index that varies between 1 and 5 (low to high shade casting ability of the canopy tree species).

Finally, the proportion of forest within a 500-m radius around each quadrat or sub-quadrat was used as a measure of habitat availability, with higher values indicating a higher amount of source habitat available within the surrounding “region”.

Appendix 2-4: Outputs from all candidate models (see main text for the list of candidate models) for each of the two compiled datasets used to analyze the observed variation in the magnitude of the coefficient estimates or slope parameter of the log(γ) variable (i.e. the response variable) in the log-ratio model (see Equation 1 in the main text) of the $\alpha \sim \gamma$ relationship (AGR): (1) $\alpha_{FS+FG} \sim \gamma_{FS+FG}$ (n = 90); (2) $\alpha_{FSorFG} \sim \gamma_{FSorFG}$ (n = 180). Linear mixed-effects models (LMMs) were used to relate the response variable against fragmentation level (frag: NF, SF, HF), spatial scale (scale: 1, 2, 3, 4), species type (sp: FS *vs*. FG) and all possible two-way interactions between all three explanatory variables (see the materials and methods section in the main text). Bold values are representing significant ($p < 0.05$) effects.

(1) slope ~ frag +scale * sp			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ (n = 90) & $\alpha_{FG} \sim \gamma_{FG}$ (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-1,0736**	**-4,2630**	**0,0005**
*frag*_HF	-0,1435	-0,8593	0,3902
*frag*_SF	0,1975	-1,1828	0,2369
scale	**0,3074**	**3,0554**	**0,0015**
***sp*_FG**	**1,2448**	**4,0842**	**0,0000**
sp*_FG:*scale	**-0,4292**	**-3,1487**	**0,0017**
R2m/R2C	0,105/0,105		

(2) slope ~ frag + scale + sp			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ (n = 90) & $\alpha_{FG} \sim \gamma_{FG}$ (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-0,6621**	**-3,0237**	**0,0011**
*frag*_HF	-0,1435	-0,8381	0,4020
*frag*_SF	-0,1975	-1,1536	0,2494
***sp*_FG**	**0,3864**	**2,7650**	**0,0058**
scale	0,1006	1,2832	0,1854
R2m/R2C	0,0601/0,0601		

(3) slope ~ frag * scale + sp			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ (n = 90) & $\alpha_{FG} \sim \gamma_{FG}$ (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
*Intercept*_NF&FS	**-0,8117**	**-2,7624**	**0,0043**
*frag*_HF	0,0275	0,0715	0,9430
*frag*_SF	0,0965	0,2511	0,8017
*sp*_FG	0,1779	1,4067	0,1615
scale	**0,3864**	**2,7549**	**0,0059**

frag_HF:*scale*	-0,0855	-0,4974	0,6189
frag_SF:*scale*	-0,1470	-0,8554	0,3923
R2m/R2C	0,0568/0,0568		

(4) slope ~ frag * sp + scale			
$\alpha_{FS/FG}$ ~ $\gamma_{FS/FG}$ [α_{FS} ~ γ_{FS} (n = 90) & α_{FG} ~ γ_{FG} (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
*Intercept*_NF&FS	-0,3575	-1,6487	0,0992
***frag*_HF**	**-0,5178**	**-2,1802**	**0,0292**
***frag*_SF**	**-0,6893**	**-2,9025**	**0,0037**
*sp*_FG	-0,1910	-0,8044	0,4212
scale	0,0927	1,3520	0,1764
***frag*_HF:*sp*_FG**	**0,7487**	**2,2291**	**0,0258**
***frag*_SF:*sp*_FG**	**0,9837**	**2,9289**	**0,0034**
R2m/R2C	0,103/0,103		

(5) slope ~ frag * sp * scale			
$\alpha_{FS/FG}$ ~ $\gamma_{FS/FG}$ [α_{FS} ~ γ_{FS} (n = 90) & α_{FG} ~ γ_{FG} (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-0,930**	**-2,430**	**0,015**
*frag*_HF	-0,366	-0,703	0,482
*frag*_SF	-0,469	-0,901	0,368
*sp*_FG	0,605	1,161	0,246
scale	**0,369**	**2,238**	**0,025**
*frag*_HF:*sp*_FG	0,788	1,069	0,285
*frag*_SF:*sp*_FG	1,132	1,536	0,125
frag_HF:*scale*	-0,076	-0,325	0,745
frag_SF:*scale*	-0,110	-0,472	0,637
*sp*_FG:*scale*	-0,398	-1,708	0,088
*frag*_HF:*sp*_FG:scale	-0,020	-0,059	0,953
*frag*_SF:*sp*_FG:scale	-0,074	-0,224	0,822
R2m/R2C	0,152/0,152		

(6) slope ~ frag * sp *			
$\alpha_{FS/FG}$ ~ $\gamma_{FS/FG}$ [α_{FS} ~ γ_{FS} (n = 90) & α_{FG} ~ γ_{FG} (n = 90)] (n = 180)			
	Coeff.	***t***	***p***
*Intercept*_NF&FS	-0,1720	-1,0015	0,3066
***frag*_HF**	**-0,5178**	**-2,1762**	**0,0296**
***frag*_SF**	**-0,6893**	**-2,8971**	**0,0038**
*sp*_FG	-0,1910	-0,8029	0,4220
***frag*_HF:*sp*_FG**	**0,7487**	**2,2250**	**0,0261**

***frag*_SF:*sp*_FG**	**0,5837**	**2,9235**	**0,0035**
R2m/R2C	0,173/0,173		

(7) slope ~ frag + sp			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ **(n = 90) &** $\alpha_{FG} \sim \gamma_{FG}$ **(n = 90)] (n = 180)**			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-0,4608**	**-3,2851**	**0,0010**
*frag*_HF	-0,1435	-0,8350	0,4037
*frag*_SF	-0,1975	-1,1494	0,2504
***sp*_FG**	**0,3864**	**2,7550**	**0,0059**
R2m/R2C	0,0478/0,0478		

(8) slope ~ frag * scale			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ **(n = 90) &** $\alpha_{FG} \sim \gamma_{FG}$ **(n = 90)] (n = 180)**			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-0,6079**	**-2,1936**	**0,0283**
*frag*_HF	0,0275	0,0701	0,9441
*frag*_SF	0,0965	0,2461	0,8056
scale	0,1702	1,3730	0,1698
frag_HF:*scale*	-0,0855	-0,4876	0,6259
frag_SF:*scale*	-0,1470	-0,8385	0,4018
R2m/R2C	0,0204/0,0204		

(9) slope ~ frag + scale			
$\alpha_{FS/FG} \sim \gamma_{FS/FG}$ [$\alpha_{FS} \sim \gamma_{FS}$ **(n = 90) &** $\alpha_{FG} \sim \gamma_{FG}$ **(n = 90)] (n = 180)**			
	Coeff.	***t***	***p***
***Intercept*_NF&FS**	**-0,4530**	**-2,4015**	**0,0163**
*frag*_HF	-0,1435	-0,8215	0,4114
*frag*_SF	-0,1975	-1,1308	0,2582
scale	0,0927	1,3002	0,1935
R2m/R2C	0,0167/0,0167		

	Candidate Models	**AIC**
1	slope ~ frag +scale * sp	504,349
2	slope ~ frag + scale + sp	509,86
3	slope ~ frag * scale + sp	516,78
4	slope ~ frag * sp +scale	505,63
5	slope ~ frag * scale * sp	511,77
6	**slope ~ frag * sp (best model)**	**501,93**
7	slope ~ frag + sp	506,13

8	slope ~ frag * scale	520,14
9	slope ~ frag + scale	513,27

(1) slope ~ frag * scale			
α_{FGFS} ~ γ_{FGFS} (n = 90)			
	Coeff.	***t***	***p***
*Intercept*_NF&FS	-0,1770	-0,8641	0,3875
*frag*_HF	-0,2483	-0,8571	0,3914
*frag*_SF	0,3582	1,2366	0,2162
scale	0,1397	1,5254	0,1272
frag_HF:*scale*	-0,0996	-0,7690	0,4419
frag_SF:*scale*	-0,2301	-1,7760	0,0757
R2m/R2C	0,157/0,157		

(2) slope ~ frag + scale			
α_{FGFS} ~ γ_{FGFS} (n = 90)			
	Coeff.	***t***	***p***
*Intercept*_NF&FS	0,0428	0,3038	0,7613
***frag*_HF**	**-0,4475**	**-3,4311**	**0,0006**
*frag*_SF	-0,1020	-0,7817	0,4344
scale	0,0298	0,5603	0,5752
R2m/R2C	0,129/0,129		

	Candidate Models	**AIC**
1	slope ~ frag * scale	158,9
2	**slope ~ frag +scale (best model)**	**153,3**

Appendix 2-5: Detailed outputs of two studied cases in the log-ratio models of $\alpha_{FS} \sim \gamma_{FS}$ (100 m^2 - 1000 m^2 and 1000 m^2 - Total patch scale) showing a significant effect of the covariate patch age.

100m² - 1000m²				
term	Value	Std,Error	t-value	p-value
Intercept	0,562	0,392	1,432	0,155
X1000	-0,086	0,121	-0,714	0,477
C:N100	0,030	0,051	0,593	0,554
pH100	-0,012	0,061	-0,197	0,844
P100	-0,003	0,055	-0,054	0,957
SCA100	0,016	0,050	0,322	0,748
for_500	**-0,225**	**0,072**	**0,605**	**0,055**
area	0,152	0,119	1,272	0,206
length	-0,041	0,117	-0,347	0,729
age	**0,436**	**0,080**	**-2,800**	**0,006**

1000m² - Total				
term	Value	Std,Error	t-value	p-value
Intercept	**-2,7833**	**0,4511**	**-6,1696**	**<0,001**
XT	**0,2731**	**0,1139**	**2,3973**	**0,0180**
C:N1000	-0,0582	0,0485	-1,1998	0,2325
pH1000	**-0,1446**	**0,0597**	**-2,4225**	**0,0168**
P1000	0,0531	0,0512	1,0372	0,3016
SCA1000	-0,0378	0,0493	-0,7660	0,4451
for_500	**-0,1430**	**0,0769**	**3,7214**	**0,0003**
area	-0,0907	0,1125	-0,8062	0,4216
length	0,0160	0,1115	0,1439	0,8858
age	**0,2840**	**0,0695**	**-2,0608**	**0,0414**

Appendix 3-1: Timeline of the different events occurring throughout the course of the experiment to prepare the right conditions for each of the eight studied treatments. Each of the eight treatments is repeated three times (i.e. three blocks).

Soil preparation	Soil cover rotation	21/07/16: Chisel plowing	21/07/16: *Camelina* / CC-mix sowing	03/08/16: 80kg/ha of N (NH4NO3)	04/17: grinding slash	04/17: deep ripping and power	04/17: round-up and anti-slug	14/06/17: 70-80kg/ha of N (NH4NO3)	29/04/17: spraying herbicide	28/04/17: sunflower sowing
Reduced tillage	***Camelina* / sunflower**									
Reduced tillage	**CC-mix / sunflower**									
Reduced tillage	**nothing / sunflower**									
Reduced tillage	**nothing / nothing**									
Direct seedling	***Camelina* / sunflower**									
Direct seedling	**CC-mix / sunflower**									
Direct seedling	**nothing / sunflower**									
Direct seedling	**nothing / nothing**									

Appendix 3-2: List of weed species used and sown at each of the 24 plots of the experimental site as well as for the three replicates in the greenhouse (cf. germination test). (Source of scientific nomenclature: J.-M. Tison, B. de Foucault et all. 2014 Flora Gallica. Ed. Biotope 1195p/)

ID	Species Name	Weight of 10 seeds (g)	Number seeds/plot
1	*Alopecurus myosuroides*	0,0243	236
2	*Amaranthus retroflexus*	0,0019	612
3	*Anchusa arvensis*	0,0031	169
4	*Apera spica-venti*	0,0049	473
5	*Artemisia vulgaris*	0,0012	2190
6	*Atriplex patula*	0,0425	102
7	*Avena fatua*	0,2389	30
8	*Capsella bursa-pastoris*	0,0023	195
9	*Cyanus segetum*	0,0321	104
10	*Chenopodium album*	0,042	165
11	*Lipandra polysperma*	0,042	92
12	*Cirsium arvense*	0,013	30
13	*Coriandrum sativum*	0,0443	75
14	*Echinochloa crus-galli*	0,0071	568
15	*Epilobium tetragonum*	0,0003	220
16	*Fallopia convolvulus*	0,0418	54
17	*Fumaria officinalis*	0,0318	115
18	*Galinsoga quadriradiata*	0,0083	101
19	*Galium aparine*	0,0835	132
20	*Kickxia elatine*	0,0087	99
21	*Linaria vulgaris*	0,0012	172
22	*Lolium perenne*	0,0092	146
23	*Matricaria chamomilla*	0,0018	748
24	*Papaver rhoeas*	0,0001	540
25	*Plantago lanceolata*	0,0043	364
26	*Plantago major*	0,0081	677
27	*Poa annua*	0,0043	67
28	*Persicaria lapathifolia*	0,1015	1
29	*Persicaria maculosa*	0,0036	116
30	*Polygonum aviculare*	0,0023	732
31	*Reseda lutea*	0,0001	120
32	*Rumex crispus*	0,0157	283
33	*Rumex obtusifolius*	0,0112	122
34	*Senecio vulgaris*	0,0002	659
35	*Silene latifolia*	0,0107	205

36	*Sonchus asper*	0,0009	191
37	*Stellaria media*	0,0362	125
38	*Tripleurospermum inodorum*	0,0001	14000
39	*Veronica persica*	0,0064	315
40	*Viola arvensis*	0,012	78

Appendix 3-3: List of candidate models together with their corresponding AIC values for the three response variables studied. Y corresponds to weed abundance or weed richness or sunflower yield (weight of seeds/stem or height).

Symbol	Candidate Model	$AIC_{abundance}$	$AIC_{richness}$	$AIC_{weight\ SF}$	$AIC_{height\ SF}$
M1	Y~ soil preparation	113,914	318,209	172,228	153,895
M2	Y~ soil cover rotation	117,046	328,705	172,137	156,351
M3	Y~ soil preparation + soil cover rotation	106,626	320,127	173,366	154,768
M4	Y~ soil preparation ∗ soil cover rotation	111,133	322,085	195,239	152,646
M5	Y~ soil preparation + block	107,853	318,424	162,256	152,499
M6	Y~ soil cover rotation + block	108,111	328,919	166,356	158,397
M7	Y~ soil preparation ∗ block	109,224	321,382	161,867	154,088
M8	Y~ soil cover rotation ∗ block	117,589	339,833	163,003	160,991
M9	Y~ soil preparation + date	113,561	318,572	nd	nd
M10	Y~ soil cover rotation + date	116,806	329,068	nd	nd
M11	Y~ soil preparation ∗ date	117,011	321,429	nd	nd
M12	Y~ soil cover rotation ∗ date	116,319	337,116	nd	nd
M13	Y~ soil preparation + soil cover rotation + block	107,357	320,342	**159,327**	156,354
M14	Y~ soil preparation ∗ soil cover rotation + block	111,839	322,299	161,814	153,154
M15	Y~ soil preparation + soil cover rotation * block	116,568	331,256	165,448	157,285
M16	Y ~ soil cover rotation + soil preparation * block	110,224	315,321	162,753	157,923
M17	Y ~ soil preparation + soil cover rotation + date	106,197	320,491	nd	nd
M18	Y ~ soil preparation * soil cover rotation + date	110,331	322,448	nd	nd
M19	Y ~ soil preparation + soil cover rotation * date	115,49	328,539	nd	nd
M20	Y ~ soil cover rotation + soil preparation * date	109,572	323,347	nd	nd
M21	Y ~ soil preparation + soil cover rotation + block + date	106,542	320,705	nd	nd
M22	Y ~ soil preparation * soil cover rotation + block + date	110,501	322,662	nd	nd
M23	Y ~ soil preparation + soil cover rotation * block + date	115,111	331,619	nd	nd
M24	Y ~ soil cover rotation + soil preparation * block + date	**104,931**	**313,664**	nd	nd
M25	Y ~ soil preparation + soil cover rotation * date + block	115,565	328,754	nd	nd
M26	Y ~ soil cover rotation + soil preparation * date + block	109,985	323,562	nd	nd

Appendix 3-4: Species germination percentage in the field versus the greenhouse. Extreme values (>100%) in the field are due to the seedbank effect. Source of scientific nomenclature: Flora Gallica (2014).

Species	Greenhouse (%)	Field (%)
Alopecurus myosuroides	14,6	5,1
Amaranthus retroflexus	n.d	1,8
Anchusa arvensis	0,6	0,6
Apera spica-venti	9,5	8,9
Artemisia vulgaris	10,4	36,9
Atriplex patula	0,3	4,9
Avena fatua	17,6	13,2
Capsella bursa-pastoris	0,5	0,5
Cyanus segetum	14,3	163,0
Chenopodium album	53,5	313,5
Lipandra polysperma	8,0	7,6
Cirsium arvense	n.d	10,0
Coriandrum sativum	39,3	113,
Echinochloa crus-galli	10,2	10957,5
Epilobium tetragonum	4,8	18,2
Fallopia convolvulus	0,6	11,1
Fumaria officinalis	0,3	44,2
Galinsoga quadriradiata	48,3	19,7
Galium aparine	21,9	90,7
Kickxia elatine	n.d	1,0
Linaria vulgaris	n.d	n.d
Lolium perenne	17,8	6,8
Matricaria chamomilla	9,4	101,5
Papaver rhoeas	n.d	0,2
Plantago lanceolata	18,5	24,5
Plantago major	1,5	0,7
Poa annua	29,5	38166,6
Persicaria lapathifolia	n.d	6287,6
Persicaria maculosa	n.d	n.d
Polygonum aviculare	n.d	7,9
Reseda lutea	n.d	6,0
Rumex crispus	n.d	n.d
Rumex obtusifolius	n.d	n.d
Senecio vulgaris	0,8	1315,9
Silene latifolia	2,4	4,9
Sonchus asper	4,2	91,6
Stellaria media	17,2	30,4

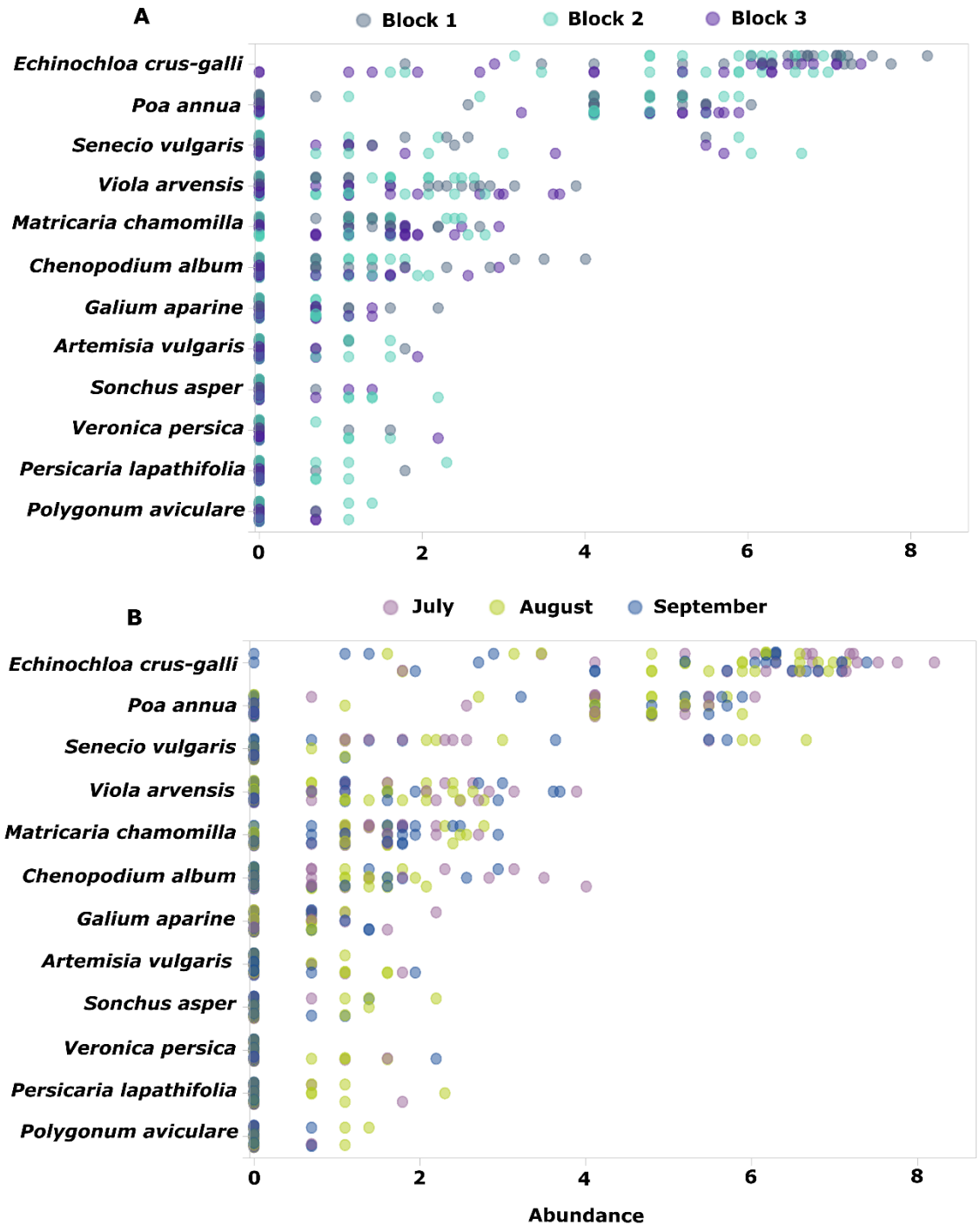
Tripleurospermum inodorum	n.d	n.d
Veronica persica	16,0	45,7
Viola arvensis	21,0	2126,6

Appendix 3-5: Weed species richness and total abundance with the difference in soil preparation, soil cover rotation, block and date in the studied 24 plots.

date	soil preparation	soil cover rotation	plot	block	Richness	Total abundance
July	direct seedling	nothing/nothing	A	1	5	1418
July	reduced tillage	camelina/sunflower	B	1	4	667
July	direct seedling	CC-mix/sunflower	C	2	8	758
July	reduced tillage	nothing/nothing	D	2	9	631
July	direct seedling	camelina/sunflower	E	3	6	200
July	reduced tillage	CC-mix/sunflower	F	3	6	55
July	direct seedling	nothing/sunflower	G	1	4	1084
July	reduced tillage	CC-mix/sunflower	H	1	7	54
July	direct seedling	camelina/sunflower	I	2	2	481
July	reduced tillage	nothing/sunflower	J	2	8	621
July	direct seedling	CC-mix/sunflower	K	3	6	89
July	reduced tillage	camelina/sunflower	L	3	10	377
July	direct seedling	CC-mix/sunflower	M	1	3	787
July	reduced tillage	nothing/sunflower	N	1	11	925
July	direct seedling	nothing/nothing	O	2	4	791
July	reduced tillage	CC-mix/sunflower	P	2	6	288
July	direct seedling	nothing/sunflower	Q	3	5	1036
July	reduced tillage	nothing/nothing	R	3	4	1025
July	direct seedling	camelina/sunflower	S	1	5	493
July	reduced tillage	nothing/nothing	T	1	8	1152
July	direct seedling	nothing/sunflower	U	2	3	22
July	reduced tillage	camelina/sunflower	V	2	8	1403
July	direct seedling	nothing/nothing	W	3	5	823
July	reduced tillage	nothing/sunflower	X	3	5	343
August	direct seedling	nothing/nothing	A	1	3	3692
August	reduced tillage	camelina/sunflower	B	1	6	1269
August	direct seedling	CC-mix/sunflower	C	2	5	448
August	reduced tillage	nothing/nothing	D	2	5	2423
August	direct seedling	camelina/sunflower	E	3	7	1156
August	reduced tillage	CC-mix/sunflower	F	3	5	345
August	direct seedling	nothing/sunflower	G	1	1	1199
August	reduced tillage	CC-mix/sunflower	H	1	8	389
August	direct seedling	camelina/sunflower	I	2	1	1619
August	reduced tillage	nothing/sunflower	J	2	5	1462
August	direct seedling	CC-mix/sunflower	K	3	9	444
August	reduced tillage	camelina/sunflower	L	3	4	201
August	direct seedling	CC-mix/sunflower	M	1	2	841
August	reduced tillage	nothing/sunflower	N	1	4	727
August	direct seedling	nothing/nothing	O	2	4	1203
August	reduced tillage	CC-mix/sunflower	P	2	4	728

August	direct seedling	nothing/sunflower	Q	3	3	907
August	reduced tillage	nothing/nothing	R	3	6	621
August	direct seedling	camelina/sunflower	S	1	4	1865
August	reduced tillage	nothing/nothing	T	1	8	565
August	direct seedling	nothing/sunflower	U	2	1	480
August	reduced tillage	camelina/sunflower	V	2	6	342
August	direct seedling	nothing/nothing	W	3	5	424
August	reduced tillage	nothing/sunflower	X	3	6	347
September	direct seedling	nothing/nothing	A	1	6	1258
September	reduced tillage	camelina/sunflower	B	1	6	556
September	direct seedling	CC-mix/sunflower	C	2	5	791
September	reduced tillage	nothing/nothing	D	2	5	795
September	direct seedling	camelina/sunflower	E	3	10	394
September	reduced tillage	CC-mix/sunflower	F	3	7	40
September	direct seedling	nothing/sunflower	G	1	2	780
September	reduced tillage	CC-mix/sunflower	H	1	9	204
September	direct seedling	camelina/sunflower	I	2	2	1200
September	reduced tillage	nothing/sunflower	J	2	6	564
September	direct seedling	CC-mix/sunflower	K	3	3	67
September	reduced tillage	camelina/sunflower	L	3	4	185
September	direct seedling	CC-mix/sunflower	M	1	3	1080
September	reduced tillage	nothing/sunflower	N	1	4	1145
September	direct seedling	nothing/nothing	O	2	4	665
September	reduced tillage	CC-mix/sunflower	P	2	3	312
September	direct seedling	nothing/sunflower	Q	3	5	309
September	reduced tillage	nothing/nothing	R	3	7	554
September	direct seedling	camelina/sunflower	S	1	4	1322
September	reduced tillage	nothing/nothing	T	1	4	491
September	direct seedling	nothing/sunflower	U	2	1	900
September	reduced tillage	camelina/sunflower	V	2	8	23
September	direct seedling	nothing/nothing	W	3	11	862
September	reduced tillage	nothing/sunflower	X	3	4	69

Appendix 3-6: abundance of weed species according to the block (A) and date (B) effects. Only most abundant species are presented.



Appendix 3-7: Detailed outputs of the best candidate model selected (see M24 in Appendix 3-3 for the model formula) at the species level to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance individually (outcomes of the "manyglm" function from the "mvabund" package). Bold values represent significant ($p<0.05$) effects (A) and their corresponding coefficient estimates (B).

A) Coefficient Table	*Alopecurus myosuroides*	*Amaranthus retroflexus*	*Anchusa arvensis*	*Apera spica-venti*	*Artemisia vulgaris*	*Atriplex patula*	*Avena fatua*	*Capsella bursa-pastoris*	*Cyanus segetum*	*Chenopodium album*	*Lipandra polysperma*	*Cirsium arvense*	*Coriandrum sativum*	*Echinochloa crus-galli*	*Epilobium tetragonum*	*Fallopia convolvulus*	*Fumaria officinalis*	*Galinsoga quadriradiata*	*Galium aparine*	*Kickxia elatine*	*Linaria vulgaris*	*Lolium perenne*	*Matricaria chamomilla*	*Papaver rhoeas*	*Plantago lanceolata*	*Plantago major*	*Poa annua*	*Persicaria lapathifolia*	*Persicaria maculosa*	*Polygonum aviculare*	*Reseda lutea*	*Rumex crispus*	*Rumex obtusifolius*	*Senecio vulgaris*	*Silene latifolia*	*Sonchus asper*	*Stellaria media*	*Tripleurospermum inodorum*	*Veronica persica*	*Viola arvensis*
(Intercept)	-14,82	-22,74	-18,21	-19,65	-2,78	-18,35	-17,85	-14,82	-11,19	0,68	-26,72	-14,82	-18,45	7,63	-1,72	-2,77	-13,61	-10,11	-15,68	-18,21	-14,82	-18,21	0,36	-14,82	-28,15	-17,85	2,42	-13,03	-14,82	-23,14	-17,85	-14,82	-14,82	-5,58	-20,73	-15,11	-20,75	-14,82	-24,95	-0,12
block2	0	0	0	0	-0,6	0	0	0	0	-0,6	0	0	0	-0,43	0,42	-10,65	0	-9,42	14,04	0	0	9,34	0,74	0	0	0	-2,19	0	0	9,75	0	0	0	-0,33	0	11,81	9,63	0	0	0,13
block3	0	0	0	10,39	1,27	0	0	0	0	-0,52	0	0	9,22	-1,48	-10,6	-10,65	0	-9,42	14,02	0	0	0	0,79	0	0	0	0,96	13,02	0	10,4	9,34	0	0	1,09	10,12	13,57	10,73	0	12,61	2,03
reduced tillage	0	11,78	0	9,98	2,02	0	0	0	10,79	-0,27	9,34	0	0	-1,02	-10,6	0,69	**12,1**	-9,42	12,94	9,34	0	0	0,98	0	0	0	1,75	14,92	0	11,35	0	0	0	-0,94	0	0	0	0	9,34	**2,19**
CC-mix/sunflower	0	9,98	8,87	10,13	2,04	-9,46	-8,87	0	-8,93	0,99	0	0	-9,58	**-1,05**	-10	-9,55	-0,41	-8,86	0,63	8,87	0	0	0,3	0	8,74	-8,87	1,45	-1,47	0	0,6	-8,87	0	0	1,09	0	1,73	9,04	0	2,2	0,44
nothing/nothing	0	9,29	0	8,75	0,2	-9,46	-8,87	0	0,69	2,05	0	0	-9,58	**0,62**	0,42	0,69	-0,41	0	0,03	0	0	8,87	0,28	0	8,74	-8,87	-0,18	-2,94	0	0,74	-8,87	0	0	3,71	10,2	0,63	10,14	0	0,38	-0,46
nothing/sunflower	0	9,29	0	0	-1,37	-9,46	-8,87	0	-8,93	0,5	8,87	0	-9,58	**0,03**	-10	0	-0,41	-8,86	1,12	0	0	0	-0,15	0	0	-8,87	-0,23	-1,19	0	-10,29	-8,87	0	0	2,48	0	-10,95	0	0	-0,59	-0,16
July	0	0	-8,51	-10,21	-0,38	9,11	0	0	-9,19	-0,46	8,51	0	9,22	-0,75	1,67	0,69	2,08	0	0,72	-8,51	0	-8,51	0,29	0	0	8,51	1,4	-0,73	0	11,14	0	0	0	**7,4**	-8,44	2,18	-9,28	0	0	-0,87
September	0	0,69	-8,51	-10,21	2,04	0	8,51	0	-0,69	-0,56	0	0	0	-0,5	-8,65	0	-9,21	9,42	0,52	-8,51	0	-8,51	-0,57	0	9,28	0	0,75	-0,54	0	11,03	8,51	0	0	**1,32**	0,69	1,25	0	0	**13**	-0,67
block2:reduced tillage	0	-1,1	0	-9,98	-0,21	0	9,34	0	-10,79	0,51	-9,34	0	0	0,64	-0,42	9,95	-1,79	18,83	-12,01	-9,34	0	-9,34	-0,59	0	0	0	1,83	-1,4	0	-11,26	0	0	0	-0,68	0	-1,37	-9,63	0	1,97	0,92
block3:reduced tillage	0	-11,78	9,34	-20,37	-1,99	9,94	0	0	-10,79	-0,09	-9,34	0	0	-0,23	10,6	-0,69	-1,1	9,42	-12,92	-9,34	0	0	-0,75	0	10,13	9,34	-0,82	-27,94	0	-11,25	-9,34	0	0	-0,77	-0,69	-3,14	-10,73	0	-10,86	-1,37

B) P-Table	*Alopecurus myosuroides*	*Amaranthus retroflexus*	*Anchusa arvensis*	*Apera spica-venti*	*Artemisia vulgaris*	*Atriplex patula*	*Avena fatua*	*Capsella bursa-pastoris*	*Cyanus segetum*	*Chenopodium album*	*Lipandra polysperma*	*Cirsium arvense*	*Coriandrum sativum*	*Echinochloa crus-galli*	*Epilobium tetragonum*	*Fallopia convolvulus*	*Fumaria officinalis*	*Galinsoga quadriradiata*	*Galium aparine*	*Kickxia elatine*	*Linaria vulgaris*	*Lolium perenne*	*Matricaria chamomilla*	*Papaver rhoeas*	*Plantago lanceolata*	*Plantago major*	*Poa annua*	*Persicaria lapathifolia*	*Persicaria maculosa*	*Polygonum aviculare*	*Reseda lutea*	*Rumex crispus*	*Rumex obtusifolius*	*Senecio vulgaris*	*Silene latifolia*	*Sonchus asper*	*Stellaria media*	*Tripleurospermum inodorum*	*Veronica persica*	*Viola arvensis*
block	1	0,986	0,986	0,986	0,986	0,986	0,986	1	0,575	0,986	0,986	1	0,901	0,078	0,986	0,953	0,986	0,986	0,078	0,986	1	0,986	0,986	1	0,925	0,986	0,986	0,986	1	0,986	0,986	1	1	0,986	0,874	0,157	0,986	1	0,974	0,953
reduced tillage	1	0,473	0,986	0,991	0,966	0,966	0,988	1	0,519	0,988	0,966	1	1	0,251	0,473	0,988	**0,04**	0,991	0,762	0,969	1	0,986	0,948	1	0,836	0,986	0,229	0,966	1	0,988	0,978	1	1	0,988	0,991	0,171	0,473	1	0,966	**0,001**
rotation	1	1	0,999	0,968	0,881	0,992	1	1	0,979	0,23	1	1	0,943	**0,038**	0,973	0,995	1	0,995	0,992	1	1	1	1	1	0,995	0,999	1	0,992	1	0,968	1	1	1	0,084	0,862	0,343	0,91	1	1	1
date	1	0,996	0,996	0,433	0,35	0,943	0,996	1	0,969	0,996	0,991	1	0,872	0,484	0,936	0,996	0,16	0,862	0,996	0,996	1	0,996	0,659	1	0,873	0,991	0,996	0,996	1	0,632	0,996	1	1	**0,001**	0,97	0,659	0,958	1	**0,012**	0,911
block:reduced tillage	1	0,997	0,997	0,417	0,943	0,974	0,997	1	0,997	0,974	0,997	1	0,997	0,943	0,997	0,956	0,997	0,925	0,925	0,997	1	0,997	0,954	1	0,997	0,997	0,865	0,201	1	0,897	0,997	1	1	0,974	0,997	0,954	0,997	1	0,417	0,343

Appendix 3-8: Weed species relative abundance with the difference in soil preparation, soil cover rotation, block and date in the studied 24 plots.

date	Soil preparation	Soil rotation	plot	block	*Alopecurus myosuroides*	*Amaranthus retroflexus*
July	direct seedling	nothing/nothing	A	1	0	0
July	reduced tillage	camelina/sunflower	B	1	0	0
July	direct seedling	CC-mix/sunflower	C	2	0	0
July	reduced tillage	nothing/nothing	D	2	0	1
July	direct seedling	camelina/sunflower	E	3	0	0
July	reduced tillage	CC-mix/sunflower	F	3	0	0
July	direct seedling	nothing/sunflower	G	1	0	0
July	reduced tillage	CC-mix/sunflower	H	1	0	0
July	direct seedling	camelina/sunflower	I	2	0	0
July	reduced tillage	nothing/sunflower	J	2	0	0
July	direct seedling	CC-mix/sunflower	K	3	0	0
July	reduced tillage	camelina/sunflower	L	3	0	0
July	direct seedling	CC-mix/sunflower	M	1	0	0
July	reduced tillage	nothing/sunflower	N	1	0	0
July	direct seedling	nothing/nothing	O	2	0	0
July	reduced tillage	CC-mix/sunflower	P	2	0	0
July	direct seedling	nothing/sunflower	Q	3	0	0
July	reduced tillage	nothing/nothing	R	3	0	0
July	direct seedling	camelina/sunflower	S	1	0	0
July	reduced tillage	nothing/nothing	T	1	0	0
July	direct seedling	nothing/sunflower	U	2	0	0
July	reduced tillage	camelina/sunflower	V	2	0	0
July	direct seedling	nothing/nothing	W	3	0	0
July	reduced tillage	nothing/sunflower	X	3	0	0
August	direct seedling	nothing/nothing	A	1	0	0
August	reduced tillage	camelina/sunflower	B	1	0	0
August	direct seedling	CC-mix/sunflower	C	2	0	0
August	reduced tillage	nothing/nothing	D	2	0	0
August	direct seedling	camelina/sunflower	E	3	0	0
August	reduced tillage	CC-mix/sunflower	F	3	0	0
August	direct seedling	nothing/sunflower	G	1	0	0
August	reduced tillage	CC-mix/sunflower	H	1	0	0
August	direct seedling	camelina/sunflower	I	2	0	0
August	reduced tillage	nothing/sunflower	J	2	0	0
August	direct seedling	CC-mix/sunflower	K	3	0	0
August	reduced tillage	camelina/sunflower	L	3	0	0
August	direct seedling	CC-mix/sunflower	M	1	0	0
August	reduced tillage	nothing/sunflower	N	1	0	1
August	direct seedling	nothing/nothing	O	2	0	0
August	reduced tillage	CC-mix/sunflower	P	2	0	0

August	direct seedling	nothing/sunflower	Q	3	0	0
August	reduced tillage	nothing/nothing	R	3	0	0
August	direct seedling	camelina/sunflower	S	1	0	0
August	reduced tillage	nothing/nothing	T	1	0	0
August	direct seedling	nothing/sunflower	U	2	0	0
August	reduced tillage	camelina/sunflower	V	2	0	0
August	direct seedling	nothing/nothing	W	3	0	0
August	reduced tillage	nothing/sunflower	X	3	0	0
September	direct seedling	nothing/nothing	A	1	0	0
September	reduced tillage	camelina/sunflower	B	1	0	0
September	direct seedling	CC-mix/sunflower	C	2	0	0
September	reduced tillage	nothing/nothing	D	2	0	0
September	direct seedling	camelina/sunflower	E	3	0	0
September	reduced tillage	CC-mix/sunflower	F	3	0	0
September	direct seedling	nothing/sunflower	G	1	0	0
September	reduced tillage	CC-mix/sunflower	H	1	0	2
September	direct seedling	camelina/sunflower	I	2	0	0
September	reduced tillage	nothing/sunflower	J	2	0	0
September	direct seedling	CC-mix/sunflower	K	3	0	0
September	reduced tillage	camelina/sunflower	L	3	0	0
September	direct seedling	CC-mix/sunflower	M	1	0	0
September	reduced tillage	nothing/sunflower	N	1	0	0
September	direct seedling	nothing/nothing	O	2	0	0
September	reduced tillage	CC-mix/sunflower	P	2	0	0
September	direct seedling	nothing/sunflower	Q	3	0	0
September	reduced tillage	nothing/nothing	R	3	0	0
September	direct seedling	camelina/sunflower	S	1	0	0
September	reduced tillage	nothing/nothing	T	1	0	0
September	direct seedling	nothing/sunflower	U	2	0	0
September	reduced tillage	camelina/sunflower	V	2	0	0
September	direct seedling	nothing/nothing	W	3	0	0
September	reduced tillage	nothing/sunflower	X	3	0	0

Anchusa arvensis	*Apera spica-venti*	*Artemisia vulgaris*	*Atriplex patula*	*Avena fatua*	*Capsella bursa-pastoris*	*Cyanus segetum*
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	2	0	0	0
0	0	0	0	0	0	0
0	0	2	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	1
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
1	0	1	0	0	0	0
0	0	0	0	0	0	0
0	1	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	3	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0

0	1	0	0	0	0	1
0	0	0	0	0	0	0
0	0	1	0	0	0	0
0	0	1	0	0	0	0
0	0	0	0	0	0	0
0	0	2	0	0	0	0
0	0	4	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	4	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	2	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	1	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	6	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	1
0	0	0	0	0	0	0
0	0	5	0	1	0	0
0	0	2	0	0	0	0
0	0	0	0	0	0	0

Chenopodium album	*Lipandra polysperma*	*Cirsium arvense*	*Coriandrum sativum*	*Echinochloa crus-galli*	*Epilobium tetragonum*	*Fallopia convolvulus*
22	0	0	0	1379	0	0
5	0	0	0	540	0	0
18	0	0	0	480	0	0
9	0	0	0	540	0	1
0	0	0	1	120	0	0
3	0	0	0	3	0	0
0	0	0	0	840	0	0
0	0	0	0	22	0	0
0	0	0	0	480	0	0
1	0	0	0	180	0	0
0	0	0	0	4	0	0
0	0	0	1	2	0	0
0	0	0	0	780	0	0
2	1	0	0	720	0	1
0	0	0	0	540	6	0
0	0	0	0	31	0	0
0	0	0	0	480	0	0
0	0	0	0	540	0	0
0	0	0	0	420	1	0
0	0	0	0	480	0	0
0	0	0	0	17	0	0
1	0	0	0	1319	0	0
0	0	0	0	31	0	0
0	0	0	0	0	0	0
32	0	0	0	3658	0	0
0	0	0	0	1259	0	0
5	0	0	0	420	0	0
16	0	0	0	2339	0	0
4	0	0	0	1079	0	0
0	0	0	0	0	0	0
0	0	0	0	1199	0	0
3	0	0	0	180	0	0
0	0	0	0	1619	0	0
3	0	0	0	1439	0	0
3	0	0	0	180	0	0
0	0	0	0	14	0	0
1	0	0	0	840	0	0
2	0	0	0	720	0	0
0	0	0	0	1199	0	0
0	0	0	0	540	0	0
6	0	0	0	900	0	0
12	0	0	0	540	0	0
0	0	0	0	1859	1	0

0	0	0	0	360	0	1
0	0	0	0	480	0	0
5	0	0	0	60	0	0
2	0	0	0	360	0	0
4	0	0	0	180	0	0
54	0	0	0	1199	0	0
1	0	0	0	420	0	0
0	0	0	0	780	0	0
0	0	0	0	720	0	0
1	0	0	0	360	0	0
1	0	0	0	6	0	0
0	0	0	0	660	0	0
4	0	0	0	120	0	0
0	0	0	0	1199	0	0
2	0	0	0	480	0	0
0	0	0	0	5	0	0
0	0	0	0	60	0	0
1	0	0	0	900	0	0
3	0	0	0	1019	0	0
0	0	0	0	660	0	0
0	0	0	0	300	0	0
2	0	0	0	240	0	0
4	0	0	0	300	0	0
0	0	0	0	1259	0	1
0	0	0	0	120	0	0
0	0	0	0	900	0	0
1	0	0	0	5	0	0
7	0	0	0	720	0	0
2	0	0	0	60	0	0

Fumaria officinalis	*Galinsoga quadriradiata*	*Galium aparine*	*Kickxia elatine*	*Linaria vulgaris*	*Lolium perenne*	*Matricaria chamomilla*	*Papaver rhoeas*
0	0	0	0	0	0	4	0
0	0	0	0	0	0	2	0
0	0	1	0	0	0	11	0
0	0	0	0	0	0	8	0
0	0	0	0	0	0	0	0
0	0	1	0	0	0	5	0
0	0	0	0	0	0	3	0
2	0	0	0	0	0	4	0
0	0	0	0	0	0	0	0
0	0	2	0	0	0	5	0
0	0	0	0	0	0	2	0
2	0	0	0	0	0	1	0
0	0	0	0	0	0	2	0
2	0	0	0	0	0	3	0
0	0	0	0	0	0	5	0
0	0	8	0	0	0	3	0
0	0	2	0	0	0	15	0
0	0	0	0	0	0	6	0
0	0	0	0	0	0	3	0
1	0	1	0	0	0	9	0
0	0	1	0	0	0	4	0
1	0	1	0	0	0	5	0
0	0	0	0	0	0	2	0
0	0	1	0	0	0	10	0
0	0	0	0	0	0	0	0
0	0	1	0	0	0	2	0
0	0	0	0	0	0	18	0
0	0	0	0	0	0	8	0
0	0	1	0	0	0	4	0
0	0	0	0	0	0	4	0
0	0	0	0	0	0	0	0
0	0	0	1	0	0	2	0
0	0	0	0	0	0	0	0
0	0	2	0	0	0	2	0
0	0	1	0	0	0	12	0
0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	1	2	0
0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	6	0
0	0	0	0	0	0	4	0

1	0	0	0	0	0	11	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	14	0
0	0	0	0	0	0	0	0
0	0	2	0	0	0	5	0
0	1	0	0	0	0	1	0
0	0	0	0	0	0	4	0
0	0	0	0	0	0	5	0
0	0	0	0	0	0	2	0
0	0	1	0	0	0	4	0
0	0	0	0	0	0	5	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	2	0
0	0	1	0	0	0	0	0
0	0	4	0	0	0	4	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	3	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	2	0
0	0	0	0	0	0	2	0
0	0	0	0	0	0	10	0
0	0	0	0	0	0	0	0
0	1	0	0	0	0	4	0
0	0	1	0	0	0	2	0
0	0	3	0	0	0	4	0

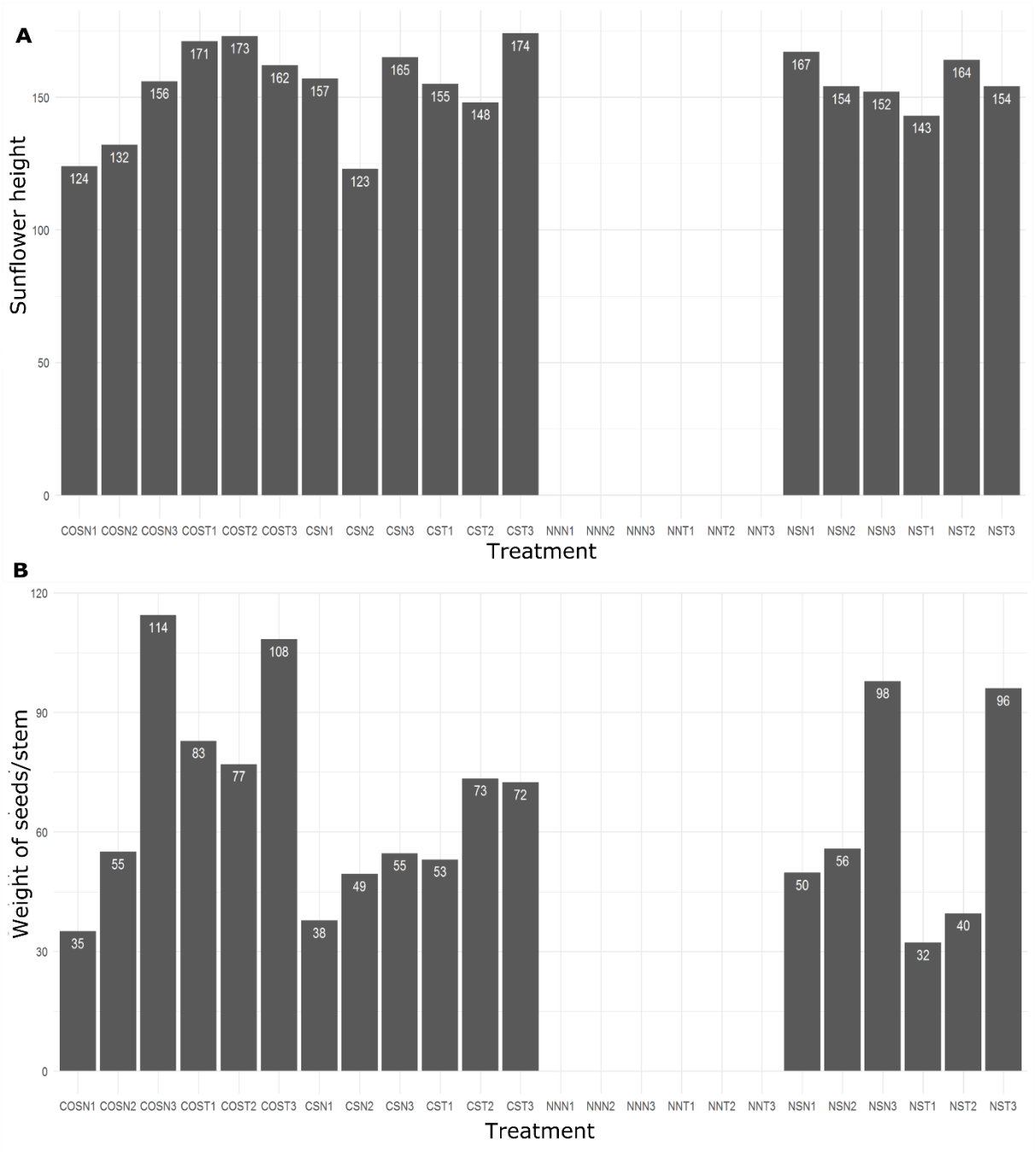
Plantago lanceolata	*Plantago major*	*Poa annua*	*Persicaria lapathifolia*	*Polygonum persicaria*	*Persicaria maculosa*	*Reseda lutea*	*Rumex crispus*	*Rumex obtusifolius*
0	0	1	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	240	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	24	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	14	0	0	3	0	0	0
0	0	0	0	0	0	0	0	0
0	0	420	1	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	1	360	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0
0	0	180	2	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	240	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	180	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	300	1	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	0	0	0	2	0	0	0
0	0	281	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	12	0	0	0	0	0	0
0	0	60	1	0	0	0	0	0
0	0	300	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	180	9	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	240	0	0	0	0	0	0
0	0	180	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	180	0	0	0	0	0	0
0	0	0	1	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

0	0	180	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	240	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	0	2	0	0	1	0	0
1	0	0	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	60	0	0	2	0	0	0
0	0	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	180	0	0	0	0	0	0
0	0	120	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0
0	0	60	0	0	0	0	0	0
1	0	240	0	0	1	0	0	0
0	0	60	0	0	0	0	0	0
0	0	360	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0
0	0	0	5	0	1	0	0	0
0	0	120	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0

Senecio vulgaris	*Silene latifolia*	*Sonchus asper*	*Stellaria media*	*Tripleurospermum inodorum*	*Veronica persica*	*Viola arvensis*
12	0	0	0	0	0	0
0	0	0	0	0	0	0
3	0	3	0	0	0	2
2	0	1	0	0	0	9
7	0	2	0	0	0	10
0	0	0	0	0	0	19
240	0	0	0	0	0	2
2	0	0	0	0	0	7
1	0	0	0	0	0	0
10	0	0	0	0	0	2
19	0	3	0	0	0	1
5	0	0	0	0	0	2
5	0	0	0	0	0	0
8	0	0	0	0	0	4
240	0	0	0	0	0	0
2	0	0	0	0	0	4
420	0	0	0	0	0	0
300	0	0	0	0	0	0
9	0	0	0	0	0	0
360	0	0	0	0	0	1
0	0	0	0	0	0	0
3	0	0	0	0	0	13
780	0	8	0	0	0	0
37	0	0	0	0	0	14
0	0	0	0	0	0	2
0	0	0	0	0	0	4
0	0	0	1	0	0	4
0	0	0	0	0	0	48
0	0	0	0	0	0	7
0	0	0	0	0	0	39
0	0	0	0	0	0	0
0	0	0	0	0	0	13
0	0	0	0	0	0	0
0	0	0	0	0	0	16
1	0	3	0	0	0	1
0	0	0	0	0	0	6
0	0	0	0	0	0	0
0	0	0	0	0	0	4
0	0	0	0	0	0	1
0	0	0	0	0	0	7
0	0	0	0	0	0	0
0	1	0	0	0	0	2
0	0	0	0	0	0	1

0	0	0	0	0	0	10
0	0	0	0	0	0	0
0	0	0	0	0	0	22
0	0	0	1	0	0	0
0	0	0	0	0	0	36
0	0	0	0	0	0	1
0	0	0	0	0	0	7
2	0	2	0	0	0	2
0	0	0	0	0	2	11
0	0	2	0	0	4	15
0	0	1	0	0	8	18
0	0	0	0	0	0	0
0	0	0	0	0	1	11
0	0	0	0	0	0	0
0	0	0	0	0	0	14
0	0	0	0	0	0	2
0	0	0	0	0	0	4
0	0	0	0	0	0	0
0	0	0	0	0	0	3
0	0	0	0	0	0	0
0	0	0	0	0	4	8
0	0	0	0	0	2	5
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
2	2	0	2	0	2	2
0	0	0	0	0	0	0

Appendix 3-9: Difference in sunflower height (A) and weight of seeds per stem (B) at different soil preparations, soil cover rotations and blocks. Abbreviations in x-axis are for the three variables: CSN corresponds to *Camelina* and sunflower rotation without tillage (i.e. direct seedling). CST corresponds to *Camelina* and sunflower rotation with reduced tillage. COSN corresponds to CC-mix with sunflower rotation without tillage (i.e. direct seedling). COST corresponds to CC-mix with sunflower rotation with reduced tillage. NNN corresponds to the soil left without both winter and summer covers and without tillage (i.e. direct seedling). NNT corresponds to the soil left without both winter and summer covers and with reduced tillage. NSN corresponds to soil left in winter and cultivated with sunflower as summer crop without tillage (i.e. direct seedling), and NST corresponds to soil left in winter and cultivated with sunflower as summer crop with reduced tillage.



Appendix 4-1: Greenhouse germination test for the 17 studied species (same species mix used to study germination success in both forest and hedgerows)

Species	**Number of germinated individuals**
Galium odoratum	0
Melica uniflora	0
Hyacinthoides non-scipta	0
Veronica hederifolia	15
Lapsana communis	5
Viola reichenbachiana	0
Oxalis acetosella	0
Lamium galeobdolon	0
Circaea lutetiana	0
Milium effusum	54
Stachys sylvatica	0
Carex sylvatica	0
Fragaria vesca	16
Stellaria holostea	12
Poa nemoralis	38
Senecio ovatus	0
Aegopodium podagraria	0

Résumé

L'absence d'une espèce dans une communauté locale alors qu'elle est présente dans d'autres communautés du même paysage peut être expliquée, soit par une limitation de la dispersion, soit par une limitation du recrutement. Le présent travail vise à évaluer la part respective de ces deux limitations dans l'assemblage de différents types de communauté. J'ai d'abord étudié la relation entre les diversités locale et proximale à différentes échelles et pour différents niveaux de fragmentation forestière dans une matrice de paysage agricole. Les résultats soulignent l'importance de l'identité des espèces lors de l'étude de l'effet de la fragmentation sur la structure de la communauté végétale. J'ai ensuite évalué le succès de la germination et la persistance d'espèces végétales à l'aide d'expériences semi-contrôlées. Dans la première expérience, j'ai étudié le succès de la germination et de la persistance d'espèces adventices des cultures semées, ainsi que leurs effets sur le rendement des cultures, sous des pratiques agricoles contrastées. Nous avons mis en évidence un effet de filtre des pratiques agricoles sur la composition locale en espèces. Dans la deuxième expérience, j'ai évalué le potentiel des haies pour servir d'habitat aux espèces herbacées forestières. J'ai semé et transplanté différentes espèces forestières dans des haies, avec et sans élimination de végétation résidente, afin d'évaluer plus avant le rôle de la compétition. Mes résultats préliminaires montrent que peu d'espèces germent et survivent dans les haies, ce qui suggère des limitations en matière de recrutement et de dispersion. Les résultats de ces travaux soulignent l'importance de la dispersion dans la colonisation de fragments surfaciques ; et du recrutement dans celle d'habitats linéaires. Les conséquences pour la conservation des écosystèmes et le maintien des services fournis sont discutées.

Mots-clés : *biodiversité, espèces forestières, fragmentation de l'habitat, limites de dispersion, limites de recrutement, règles d'assemblage des communautés, pratiques agricoles, végétation.*

Summary

The absence of a given species in a local community despite its presence elsewhere in the landscape may be due either to dispersal limitation or to recruitment limitation. The aim of the thesis is to evaluate the respective importance of these limitations on community assembly. I first investigated the relationship between local and proximal diversity at different scales and for different forest fragmentation levels in an agricultural landscape. Results highlight the importance of considering species identity when studying the effect of fragmentation on plant community composition. I then assessed the germination success and persistence of vascular plant species using semi-controlled experiments. In the first experiment, I monitored the germination success and persistence of sown weed species, and their subsequent effect on crop yield, under contrasted agricultural practices. I evidenced a sorting effect of agricultural practices on local plant species composition. In the second experiment, I assessed the potential of hedgerows to serve as habitats for forest plant species. I sought seeds and transplanted seedlings in hedgerows to monitor germination and persistence, respectively, each time with and without removing the resident vegetation to further assess the role of competition. My preliminary results show that few species germinate and survive in hedgerows, suggesting that both recruitment limitations are at play. Results from this work emphasize the importance of dispersal in the colonization of habitat; and of recruitment in the colonization of linear habitats. I finally discuss the consequences of these results for ecosystem conservation and for maintaining the delivered services.

Keywords: *agricultural practices, biodiversity, community assembly rules, dispersal limitation, forest plant species, habitat fragmentation, recruitment limitation, vegetation, habitat fragmentation*