

Edge effects on plant species diversity in forest landscapes

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Cover: Forest edge facing agricultural land, the county of Södermanland, Sweden. Photo: Tiina Vinter, 2010

Summary

The forest interior and the forest edge are different due to the characteristics of the adjacent land cover surrounding the edge. When large forest areas are divided into smaller fragments the interface between the forest interior and surrounding environments increases and various processes start affecting remaining forest ecosystems and forest species. Urban or rural landscapes, cultivated monocultures or grasslands can influence the edge regions differently.

This review is focusing on edge effects in forested environments. Edge effects on plant species diversity and species composition are expected to vary according to forest patch size, patch configuration and placement in the landscape. In general, edge effects are expected to have higher impact on species diversity and composition when the remaining forest patches are small, have an irregular shape or when the surrounding land use is significantly different from the forest patch. Edge effects depend on both biotic and abiotic factors, applied management regimes and on land use history. Further studies on landscape level can shed more light on the underlying mechanisms generating the observed patterns.

Sammanfattning

De inre partierna av en skog skiljer sig från kanten då skogskanter i stor utsträckning återspeglar landskapet utanför skogen. När stora skogsområden delas i mindre fragment ökas kontaktytan med omgivningen och olika processer börjar påverka de återstående skogsekosystemen och de skogsarter som finns i de delade skogspartierna. Skogskanter kan se väldigt olika ut beroende på om de vetter mot stadsmiljö, lantbruk, fält med monokulturer eller betesäng.

Denna sammanfattning fokuserar på kanteffekter i skogslandskapet. Mångfald och artsammansättning av kärlväxter i skogen påverkas av kanteffekter genom skogens storlek, form och placering i landskapet. Generellt förväntas kanteffekter påverka växternas mångfald och artsammansättning mer när skogarna är små, har oregelbunden form eller när det omgivande landskapet skiljer sig mycket från skogsmiljön. Effekten är beroende av både biotiska och abiotiska faktorer, rådande skogsbruk och skogens historia. Ytterligare studier på landskapsnivå kan hjälpa till att belysa de underliggande mekanismerna som skapar de mönster vi ser idag.

Introduction

Patterns in the landscape

Present patterns of forested areas in the landscape in the Baltic Sea region are to a large extent formed by anthropogenic processes. Prior to human settlements the landscape was primarily forested. Through the history of human land use, the landscape has been turned into a mosaic of rural and agricultural landscapes. One of the most striking changes, that have occurred over the last century all over the world, is that forest ecosystems have become more and more fragmented as continuous natural forests have been divided into smaller patches which are spatially separated by forestry or other types of land use, leading to an increased amount of edge and edge-influenced habitats (Riitters et al., 2000; Skole and Tucker, 1993). It has been shown that the introduction of clear cutting practises in the 1950s has led to increased amount of edges in the forested landscape (Lofman, 2007; Lofman and Kouki, 2001). However, an opposite trend during the last 20-30 years is the increasing number of monocultures of tree plantations due to an increasing demand for wood products and an increasing popularity of industrial bio-energy. This development is a consequence of national subsidy schemes in Europe on wood as a renewable resource. A process accelerating the creation of new edges and fragmentation (Global Forest Coalition, 2010). At the same time there is growing awareness about environmental and biodiversity matters. For example in Sweden today 79.5% of the forested land is made up by productive forests, where production is at least 1 cubic meter per hectare and year. 3.1% of this productive forest land is within protected areas with restricted management and cutting regimes (Swedish National Forest Inventory, Forest statistics, www.slu.se/sv/webbtjanster-miljoanalys/statistik-om-skog/arealer/) and the rest is managed according to the Swedish Forestry Act (Swedish Forest Agency).

A forest patch has an edge and an interior area, the edge acts as an interface between the forest and the surrounding matrix. A large forest has a low edge/interior ratio. As a forest decreases in size there will be a subsequent increase in the edge/interior ratio. In this paper I will discuss how forest plant species are influenced by this ratio, known as edge effect (Murcia, 1995) or Edge Influence (EI) (Harper et al., 2005). Some species will disappear while others become more abundant according to changed environmental conditions (Brothers and Spingarn, 1992; Fox et al., 1997; Fraver, 1994; Honnay et al., 2002c). Species composition can also be homogenized

due to dispersal limitations in many species (Honnay et al., 2002b). Different mechanisms of edge effects, primarily effecting plant species in forest environments, will be reviewed in this work.

Edge effect

An edge is an interface between two different types of environments or ecosystems, arising between two different landscape forms or habitats - like a border between a spruce forest and a barley field. Edges between different landscape forms can form naturally but many edges in Europe today are created by anthropogenic activities like logging and road building (Linke, 2007). Large forest areas have been divided into regularly shaped fragments, often with unnatural straight borders, as a consequence of crop field formation on former forest land and by the expansion of pasture land, settlements and urban areas (Moser et al., 2002). As large forest patches are fragmented the relative length of the edge to interior areas is increased and edge effects become more pronounced. The reduction of patch size is thereby accompanied by a relative increase in the length of edge in forest habitat fragments creating the periphery of forest habitat that differs from the interior due to the influence of adjacent habitats. As a consequence structural differences between the edge and the interior area are causing edge effects (Gonzalez et al., 2010; Hamberg et al., 2008; Laurance, 1991b; Meiners and Pickett, 1999; Murcia, 1995).

The first report on edge effects came already 1933 showing that edge habitats had a higher abundance and diversity of game species and therefore had a positive effect on species diversity (Leopold, 1933). Later on, studies both on positive, neutral and negative effects of edges on species diversity have been published (Gascon et al., 2000; Gates and Gysel, 1978; Laurance et al., 1998; Laurance et al., 2002; Leopold, 1933). In general it can be concluded that edge effects are expected to have higher impact on species diversity when remaining forest patches are small, have an irregular shape or when the surrounding land use is significantly different from the forest patch.

At the forest edge both biotic and abiotic conditions are changed – first of all there is increasing amount of light penetrating into the forest from the borders effecting for example seed

germination and plant survival rates. South facing edges commonly receive more sunlight than North facing edges, influencing temperature and moisture parameters. Moisture and wind conditions can also be affected by the orientation of the edge causing changes in stand composition and structure by elevated rates of falling trees on edges exposed to frequent winds or tree mortality caused by damp weather conditions (Chen et al., 1992; Laurance, 1991b).

There are many different mechanisms that generate edge effects for vascular plant species. One example is that abiotic conditions at the edge can affect the quantity, quality and the dispersal patterns for seeds. Many studies have shown higher predation rates in habitat edges (Donoso et al., 2004; Restrepo and Vargas, 1999; Roach et al., 2001; Tallmon et al., 2003). For example higher predation on seeds has been recorded as a consequence of higher abundance of mice at forest clear cuts, leading to decreasing plant recruitment and thereby reduced population size at forest edges (Jules and Rathcke, 1999). Dispersal of seeds on the other hand can be favoured at edges because seed dispersal is usually facilitated by generalist birds usually favoured by forest edges (Watson et al., 2004).

Population viability of plants has been shown to be affected by herbivores and diseases that spread more easily along the edge, making plants more vulnerable for attack as they become easily accessible on forest edges (Chen et al., 1992; Saunders et al., 1991). It is generally assumed that ecological responses mentioned earlier will be weaker at “soft” edges than near “hard” edges (Stamps et al., 1987). Edges are called to be soft if the forest interior habitat is similar to the exterior matrix and hard if there is a large contrast between the two environments. The strength of the responses can be explained by the differences in mean vegetation height and vegetation densities forming edges with varying permeability for light and wind factors resulting in different rates of ecological flows (Duelli et al., 1990; Stamps et al., 1987). Thereby habitat edges have the potential to influence everything from species evolution (Smith et al., 1997) to ecosystem functions (Klein, 1989) by altering species interactions, ecological mechanisms, patterns and dynamics at different spatial scales (Gosz, 1993). In general ecological processes are expected to be more variable and extreme on edges than in forest interiors due to changed environmental conditions (Ewers and Didham, 2006).

Species respond in various ways to edge effects - some species become more abundant while others show no response or decline. Edge habitats can affect species in a positive way both by changed microclimate on the forest edge and the availability of resources from two surrounding habitats providing environmental heterogeneity (Tscharntke et al., 2002). Many weed species are positively affected by edge environments leading to higher species richness on forest edges. Edge effects are considered to have a negative effect when changes at the edge start to influence species in the core area that are dependent on forest interior conditions. Species that are area-sensitive and extinction-prone are extra vulnerable to edge effects, for example when weedy species disperse from the edge areas to core areas of a forest patch (Burkey, 1995; Ferraz et al., 2003). Seeds of weed species (*Taraxacum spp.*, *Articum spp.*, *Prunella spp.*) are carried into forest interior by wind and can eventually change the composition of the forest interior flora as weed species are often responding faster to changes in the environment (Alverson, 1994).

Edge effect can sometimes be masked or even enhanced through confounding factors like further fragmentation of the habitat, diminishing fragment area (thereby diminishing interior area), disadvantageous fragment shape, fragment isolation and matrix structure (Ewers and Didham, 2006). Synergies between all those effects are extrinsic drivers of forest species population decline and can magnify the detrimental impacts of each effect on species decline. In many cases it can take decades before the full effects of those processes will be expressed. Accordingly, as Ries and Sisk (2004) also conclude, much of the inter- and intraspecific variability observed in the literature concerning edge effects can be explained by habitat quality, resource distribution between habitat fragments and surrounding matrix and regional variation in resource use.

Ecological processes on the edge

Species composition on habitat edges is the consequence of ecological processes and so far several mechanisms have been proposed to explain the patterns observed. All species on the edges can experience positive, neutral or negative edge effects depending on the edge type (Ries and Sisk, 2004) with respect to distance from the habitat edge. Species experiencing edge effects either increase near the edge (positive edge response), do not change (neutral responses), or decreases near the edges (negative responses). Species are also expected to react with varying

sensitivity to edges according to their life history or ecological traits - dispersal abilities, available defence mechanisms against herbivores and the scale at which they perceive the landscape or habitat quality (Ries and Sisk, 2004). Observed edge effects might arise through complex interactions among different mechanisms. Ries and Sisk (2004) present a unified model with four mechanisms that are underlying the edge effects and changing abundance patterns: ecological flows, access of resources in scattered habitat landscape, resource mapping and species interactions. Their model describes how the distribution of organisms, and thereby ultimately even the community structure, is altered by near habitat edges. Mobile organisms can have better access to resources scattered in the landscape, when they are closer to edges as they map onto changes in the distribution of their resources. This change of species distribution near edges can lead to novel species interactions further influencing abundance and distributions of these species. Finally an altered community structure near edges is a consequence of all these changes in species distribution.

Honnay *et al.* (2002c) recognized the need for more exact measurement and quantification methods of edge effects to identify mechanisms behind the homogenization pattern observed. They defined effective edge widths (i.e. depth of edge influence), the distance that separates the edge and core zones in a forest (Honnay *et al.*, 2002c). Later also a measure for Edge Influence (EI) to estimate edge effects magnitude and distance from the border to interior areas was introduced (Magnitude of Edge Influence, MEI and Distance of Edge Influence, DEI) to quantify the edge effect (Harper *et al.*, 2005). This way of considering edge effects has led to better understanding of ecological processes shaping forest edge vegetational patterns. The EI is expected to be low and less ecologically important in landscapes with high degree of inherent heterogeneity while high EI leads to homogenization of species through various mechanisms like primary and secondary edge responses (Harper *et al.* 2005) (Fig. 1). Primary ecological responses are direct damage to trees and vegetation, disruption of the forest floor and changes in evapotranspiration rates, nutrient cycling and decomposition (Harper *et al.*, 2005). These processes change the forest structure: –the canopy cover, tree density, number of fallen trees, leaf area and vegetative biomass. Secondary responses, that are consequences of primary responses like decreasing recruitment due to loss of flowers, lower growth rate due to herbivory etc.

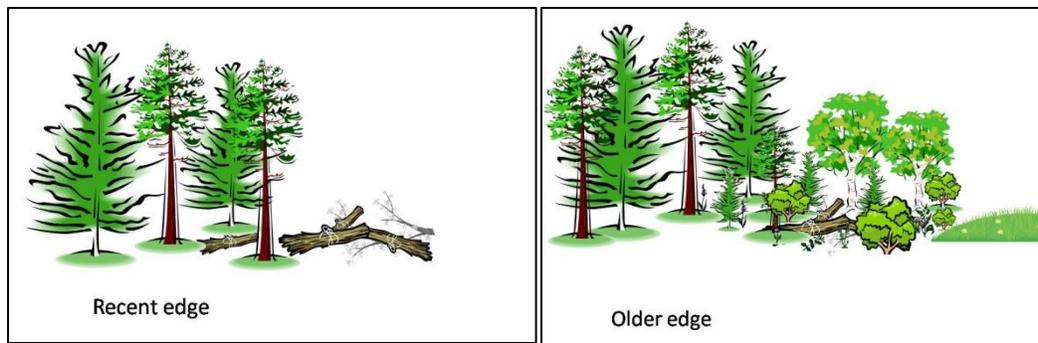


Figure 1: Species composition on forest edge as a response to processes in time following edge creation. (Modification from Harper *et al.* 2005)

Forest structure can be altered further through increased understory tree density, shrub cover and changes in species composition. The distance of edge influence from the edge to forest interior can become steeper, weaker or longer at older edges through edge sealing, softening or expansion. The edges will be sealed as the dense vegetation develops at edges, there will be higher magnitude of edge influence and the distance of edge influence will be shorter. As the vegetation regenerates the edges become softer by the reduction of edge influence due to structural changes, low magnitude of edge influence and short distance of edge influence into the forest interior. Edge influence extent can also expand as the extent of the edge influence can increase over time, the magnitude of edge influence is low but the distance of the edge influence is high. Both abiotic and biotic influences are expected to change in forest edges and may diminish in time but Harper *et al.* (2005) expects structural and compositional responses to sustain. Changes to understory structure and species composition through primary and secondary processes will thereby combine with the influence of the original edge gradient and will become a continuous development of the new edge habitat.

Populations in habitat edges are largely affected by ecological flows of energy, matter and organisms from adjacent habitat patches and the surrounding matrix (Ewers and Didham, 2006). Edge permeability, depending on the plant structure of the edge, is an influential factor for ecological flows (Strayer *et al.*, 2003). Ries and Sisk (2004) earlier presented a conceptual model based on resource distribution to explain patterns and variability observed in nature. Their model predicts decreased abundance in preferred habitat and increase in non-preferred habitat when resources are found predominantly in one habitat; increase occurs near both edges when

resources are divided between habitats; neutral edge response is expected when resources are spread equally among habitats and increase in abundance when resources are concentrated along the edge. Due to this flow of exchanged material, organisms and energy between patches (Cadenasso et al., 2003; Wiens et al., 1985), organisms with broad habitat requirements may gain from edge formations as different habitat types with ecologically different resources become available (Dunning et al., 1992; Fagan et al., 1999; Leopold, 1933; McCollin, 1998).

Based on both empirical and theoretical studies, Fagan *et al.* (1999) propose four principal classes of edge-mediated effects on species interactions based on a partial differential equations (PDE) framework. The partial differential equations are used as a tool to include the effects of habitat edges on population demographics and species interactions. More detailed descriptions of PDE are provided in Okubo (1980), Murray (1993) and Holmes *et al.* (1994).

Fagan *et al.* (1999) divide these effects into four classes.

Class 1: Species interactions can be changed on edges by altered species` movement patterns. Habitat edges facilitate or restrict the dispersal of organisms or their propagules thereby altering the intensity of particular species` interactions and impacting community dynamics.

Ex.: Habitat boundaries restricted pollen flow among plants as a consequence of the changed movements of pollinators, finally reducing the neighborhood size of reproductive individuals (Aizen and Feinsinger, 1994). Equally altered plant compositions has been reported in forest fragments as a consequence of edge-mediated change in

Class 2: Edges can change community dynamics by differentially inducing species` mortality. Unbalanced edge-mediated mortality among species can alter species interactions and influence plant competitive dynamics.

Ex. Microclimate on edges can be considerably different from core areas (for example sharp forest edges) causing higher mortality of plant seeds and seedlings (Janzen, 1983; Saunders et al., 1991). Janzen (1983) showed how the germination of native tree species was hindered by the

altered germination of tolerant weed species leading to more pronounced dissimilarities between intact forests and fragmented forest regions.

Class 3: Edges can alter species interactions through cross-boundary subsidies. Cross-boundary subsidies influence the outcome of species interactions relating to source-sink dynamics and includes ecological trap hypothesis, dispersers` impacts on residents of one patch type are subsidized by their feeding and reproductive activities in another patch.

Ex. Nesting passerine birds prefer forest edges to forest interiors as they find increased foraging areas but they experience increased mortality on forest edges as edge-foraging generalist predators and nest parasites are more common in those habitats resulting in an ecological trap for a large fraction of bird populations. (Gates and Gysel, 1978)

Class 4: Edges can create new opportunities for species interactions. Species interactions are generated on edges as edges provide a new unique habitat type creating possibilities for interactions between species that would not interact otherwise.

Ex. Edge-dependent browsing influences the successional propagation of forest edges across landscapes (Hardt and Forman, 1989); animal “travel lines” on edges generate high frequency of interspecific contacts (Angelstam, 1986; Gates and Gysel, 1978; Kaiser, 1983) and opportunities for interspecific competition are created (Laurance, 1994; Summers and Underhill, 1996).

In conclusion the processes acting on any given edge are dependent on ecological processes acting on specific edge habitats and are influenced by ecological flows of material, resource availability, species interactions and the temporal aspect of the successional stage and are thereby context-specific.

Shape and area relationships

Edge effects are expected to be more influential when fragments are small or irregularly shaped (Forman, 1986). Therefore, the relationship between edge and core area becomes an important

issue. The edge effect is not addressed sufficiently by island biogeography theory (MacArthur, 1967) even though, it concentrates on colonization and extinction mechanisms as the main explanatory factors generating the structures and patterns observed in a given habitat.

It is commonly accepted that the ratio between the perimeter length and the area of fragments (p/a) takes both the size and the shape variation into account (Buechner, 1987; Forman, 1986; Schonewald-Cox, C. M. and Bayless, 1986; Stamps et al., 1987). There are problems with this simplification because it does not take the edge effect influence and its strength into account. A core-area model that is introduced by Laurance (1991b) helps to estimate the total area of the core habitat within fragments. This model uses two parameters to estimate the edge function in addition to the area and the perimeter length of the fragment studied. When considering the effect of edges, Laurance (1991b) showed that there is a critical range of fragment sizes where the impact of edge effects increases exponentially for any edge-sensitive species and habitat type. Fagan *et al.* (1999) also pronounce the importance of the relative extent of core habitats to the maintenance of biotic diversity within a patch. Considering only the distance to nearest edge, as proposed by Malcolm (1994), can be misleading indicator of the extent of unaltered core habitat remaining in a patch. Hela detta stycke är svårt att förstå och med lite underliga meningar

According to earlier argumentation small fragments lose a large proportion of its core area when circular shape is turned into more irregular shape (Laurance et al., 2006). Forest interior habitats particularly gain from compact patch shapes because of the low edge-to-interior ratios. In contrast convoluted and elongated patches, have larger proportion of edge habitat than core habitat compared to circular forms (Kupfer, 1995; Kupfer et al., 2006; Laurance, 1991a). And as mentioned earlier, shape and area of a fragment are strongly correlated (Cochrane and Laurance, 2002; Watson, 2003). Forest patches with irregular patch shapes have been observed to have higher species richness as the edge environment provides suitable microclimate and habitat for several different species (Honnay, 1999). This kind of forest patches are found to contain more anemochorous (wind dispersed) plant species (Dzwonko and Loster, 1988). Varying results from studies concerning patch shape indicate that patch shape and area per se cannot be used to determine species richness (Dzwonko and Loster, 1992). According to Honnay *et al.* (2002a) a combination of edge shape (edge index), area of the patch and the penetration depth provides the basis for calculation of undisturbed core area of the patch and allows to compare that to the area

of the edge. Several other complexity indices are used to predict plant species richness like shape index, fractal dimension and comparison to the area of minimum bounding rectangle. Moser *et al.* (2002) introduced an index to measure the complexity of landscape patch shape to predict species richness of vascular plants and bryophytes. Species richness decreases with the increasing land use intensity as human land use leads to more simple, rectangular and rectilinear shapes in the landscapes (Forman, 1986; Forman, 1995; Krummel *et al.*, 1987; O'Neill *et al.*, 1988; Rex and Malanson, 1990). The index is calculated with the help of GIS program and is based on the minimum number of points it takes to characterise the boundaries of individual patches in the landscape based on aerial photographs, it is called the number of shape characterising points (NSCP)(Moser *et al.*, 2002) .

The shape and the area of the edge and core are important and dependent on each other. There are several indices and models to consider and apply to resolve the questions at issue in every actual site and study. There are also new methods being developed as the knowledge about landscape configuration and the techniques to measure this complexity becomes further developed and commonly used, e.g. using GIS.

Other characteristics of the edge

Species, ecosystems and processes in the forest interiors are affected by edge effects through fragmentation, changed light conditions causing warmer and drier microclimate, reducing interior habitat quality and overall habitat quantity, and isolating the remaining interior habitat which can restrict dispersal of organisms (Bannermann, 1998).

The descriptions of vegetation responses to edge influence vary a lot in the scientific literature. That is implying that all edges should not be considered to effect vegetation equally (Alignier and Deconchat, 2011). The degree of edge influence depends on edge characteristics like age, structure, orientation, adjacent land-use, etc, and the depth of edge influence on vegetation can vary from 15 m (West *et al.*, 1981) to over 1000 m (Bannermann, 1998; Honnay *et al.*, 2002b; Laurance, 1991a; Laurance, 1991b; Matlack, 1993), although it generally does not exceed 50 m in temperate forests (Honnay *et al.*, 2002b).

Canopy penetrating light properties are often measured in studies as an abiotic variable that is both easy to acquire, important for plant species in forest environments and most likely modified by the edge effect (Devlaeminck et al., 2005b; Weathers et al., 2001). As light properties are changed on forest edges following structural changes, temperature and humidity conditions are also changed. In stands of old-growth Douglas-fir forest in Pacific Northwest USA, edge effects caused by temperature and humidity were detected from 30 to over 240 m from the edge. The depth of the edge effect also depended on edge orientation and depth of wind influence, which in turn was largely influenced by vegetation type, type of understory and stand density (Chen et al., 1995).

The influence of edge orientation on edge effects (Honnay et al., 2002c; Thimonier et al., 1992) is more pronounced on south and west-facing edges (Brothers and Spingarn, 1992; Burton, 2002; Chen et al., 1995; Jose et al., 1996; Matlack, 1993; Murcia, 1995; Palik and Murphy, 1990). Ries and Sisk (2004) also predict that edge orientation effects should differ at different latitudes. In northern temperate zones we should expect south facing edges to experience stronger edge effects, because these edges are more exposed to sunlight. Edge effects are expected to be more pronounced due to changes in microclimatic patterns than to vegetation changes.

Edge vs. interior

Area and isolation effects

Edges are most commonly created by fragmentation of habitats and habitat fragmentation has been suggested to be one of the most important threats to species diversity (Honnay et al., 2005; Kellman, 1996; Wilcox and Murphy, 1985). Habitat fragmentation increases the total length of edge habitat that substantially differs from core habitat as biotic and abiotic conditions there are changed. When large coherent habitats are divided into smaller isolated fragments, the landscape becomes fragmented with small habitat patches that have been modified to various extent by humans, and thus differing from its original habitat conditions (Ranta et al., 1998). According to Opdam and Wiend (2002) a habitat becomes fragmented when the continuity in a habitat is lost – both the physical continuity and the landscape ability to ensure the dispersal of species between

the habitat fragments (Langlois et al., 2001; Opdam, 2002). At a landscape level connectivity is affected both by the pattern of fragmentation and the quality and characteristics of the surrounding matrix (Baskent and Jordan, 1995). All landscapes are naturally heterogeneous as gaps are created by windfalls, wildfires or flooding, but natural fragmentation is operating at smaller temporal and spatial scales and has a higher degree of connectivity than human generated fragmentation.

Distance from the ancient-recent woodland boundary has been found to be an important factor for the occurrence of woodland species and the species composition (Brunet et al., 2000; Dzwonko and Loster, 1989); dispersal of particularly forest plants is found to be more successful in landscapes where connectivity is high and forest fragmentation is low (Honnay et al., 2002b). The possibility to maintain connectivity in fragmented landscapes is higher in landscapes that contain few large fragments in a clumped distribution (With et al., 1999a; With and King, 1999b) allowing distribution of species between all habitat patches that are suitable, are in close range and are of favourable size, at any given time reducing the likelihood of extinction threshold to occur.

It has been reported that species extinction thresholds varies between species and landscapes (Summerville and Crist, 2001; With and King, 2001). According to metapopulation theory a metapopulation is dependent on both habitat area, quality and spatial arrangement in a landscape (connectivity limitations) (Ovaskainen, 2004) due to demographic or environmental stochasticity (Casagrandi and Gatto, 1999; Casagrandi and Gatto, 2002). The metapopulation concept has been shown to have a good explanatory value for understanding species dynamics in fragmented landscapes (Hanski, 1999) and is considered to be the most productive theoretical framework to study regional population dynamics and to understand large-scale population dynamics, spatial distribution of species, dynamics of species interactions and the effect of habitat fragmentation on biodiversity (Ouborg, 2004).

Verheyen *et al.* (2004) proposes a new model (Eq. 1) as a modification to Hanski's Incidence Function Model (IFM) to count for destruction and creation of habitat patches thereby considering landscape dynamics, besides species dynamics, as the most characteristic process of many human-dominated landscapes. The use of fitted values for IFM models allows analyzing

biologically meaningful parameters that can be used to project metapopulation dynamics under a range of scenarios.

$$J_i(\text{age}) = \frac{C_i - C_i(1 - C_i - E_i)^{\text{age}}}{C_i + E_i}.$$

Equation 1. Modified IFM model according to Hanski (1994) incorporating landscapes dynamics. J – patch occupancy, C – colonization per unit time, i – given habitat patch, E – probability of going extinct. (From Verheyen *et al.* 2004)

Empirical evidence shows that isolated small plant populations in fragmented habitat can suffer from inbreeding and genetic drift (Leimu *et al.*, 2006; Paland and Schmid, 2003; Willi and Fischer, 2005). Small populations show higher fitness gain from outbreeding compared to large populations for obligate outbreeding plant species (Bossuyt, 2007; Willi and Fischer, 2005). Clonal forest plant species, like *Paris quadrifolia* (Jacquemyn *et al.*, 2006) and *Maianthemum bifolium*, risk to evolve into remnant populations with low levels of genetic variation and limited sexual reproduction in heterogeneous environments in fragmented landscapes (Honnay *et al.*, 2006). Thereby fragmentation affects both organisms and processes at different levels and time scales.

Species richness

Several authors have reported increased species richness at the forest edges compared to core areas (Devlaeminck *et al.*, 2005a; Gehlhausen *et al.*, 2000; Guirado *et al.*, 2006; Honnay *et al.*, 2002b; Marchand and Houle, 2006) and higher variability in species richness in the edge zone (Marchand and Houle, 2006). Some specific species groups like alien plant species (Brothers and Spingarn, 1992; Fraver, 1994), colonizing plant species (Fox *et al.*, 1997) pioneer and weedy (shade intolerant and competitive) plant species (Honnay *et al.*, 2002c) tend to become more common near edges and are scarce or absent in the forest interior (Godefroid and Koedam, 2003). Only a few species have the ability to penetrate forest interiors as they are “stress tolerant

competitive” according to Grime (1988), Honnay *et al.* (2002b) reports *Rubus fruticosus* coll. and *Urtica dioica* to penetrate furthest into the forest.

In general local species richness is expected to decrease with decreasing habitat patch area and increasing isolation of the patch (Fahrig, 2003; Hanski, 1999; MacArthur, 1967). Species response to habitat loss and fragmentation can be explained with specific life-history traits of species that limit their ability to adapt to changing environment (Ewers and Didham, 2006; Henle *et al.*, 2004; Prugh *et al.*, 2008). Landscapes that are highly fragmented are expected to become similar in species composition, dominated by few generalist species with similar traits (Ekroos *et al.*, 2010; McKinney and Lockwood, 1999). Öckinger *et al.* (2010) conclude that variability in species responses to fragmentation that have been recorded in the literature (higher species richness accompanying increasing edge areas and fragmentation) may be due to species life-history traits associated with dispersal, niche breadth and reproduction. Habitats in highly fragmented landscapes dominantly contain generalist species with good dispersal abilities and high reproductive rates (Öckinger *et al.*, 2010). Diminishing forest area and increasing fragmentation is thereby expected to lead to decreased species diversity and increased homogenization.

There have been attempts to predict vascular plant species richness in different types of forests using environmental variables like habitat diversity, forest age and forest area – some of the useful tools for forest management and biodiversity conservation work. Some indicator species are used to evaluate species richness - species with high diversity of dispersal strategies. Species that are found to be indicators of high species richness in forests are autochorous species, having motile spores or propagules disseminated by the parent plant (*Oxalis acetosella*), myrmecochorous – seed dispersal by ants (*Lamiastrum galeobdolon*), anemochorous – dispersion by wind (*Milium effusum*) or endozoochorous – dispersal by animals (*Maianthemum bifolium*). Species-poor forests are dominated by endozoochorous species (Dumortier *et al.*, 2002). Other important factors predicting species richness as mentioned earlier are habitat diversity and quality.

As a consequence of all the processes and factors mentioned earlier, increasing global biotic homogenization is expected (McKinney and Lockwood, 1999) as generalist species are expected

to tolerate ongoing climate changes better than species with specific habitat demands (Schweiger et al., 2010) and as further habitat fragmentation is threatening the function and resilience of ecosystems (Potts et al., 2010).

Forest species

Forest species are adapted to conditions of forest core - according to Ellenberg scores a forest species list has been proposed by Hermy *et al.* (1999) for European forests. Forest species in contrary to edge species are often described as shade- or semi-shade tolerant plants, pure competitors, they often have large seeds that presumably have higher germination capacity under shaded circumstances (Hodkinson et al., 1998) and as shady and litter rich ground layers in deciduous woodlands are expected to select for large seed size (Bierzuchudek, 1982; Salisbury, 1942), they prefer moderate soil moist and intermediate pH and nitrogen availability. Most forest species are long-lived perennials often reproducing clonally, they have long generation time and that can make them more vulnerable to environmental changes as they can postpone the sexual reproduction while waiting for more suitable conditions (Bierzuchudek, 1982; Cain and Damman, 1997; Ehrlen and Lehtilä, 2002; Inghe and Tamm, 1985). 85% of all European herbaceous forest plants are shown to have clonal propagation (Klimes, 1997) and low light conditions are shown to suppress further sexual recruitment and trigger clonal growth (Lezberg et al., 2001; Verburg and Grava, 1998).

The ratio between sexual and clonal reproduction is expected to be biased by habitat fragmentation. Opportunities for successive pollination for outcrossing species decreases with increasing isolation of patches, and more species can become dominantly clonally reproducing (Brys et al., 2003; Honnay and Bossuyt, 2005; Hooftman et al., 2003; Rossetto et al., 2004). There are several advantages with clonal reproduction as clonal plants appear to be more tolerant for extinction events, less affected by environmental and demographic stochastities and are better buffered against spatio-temporal heterogeneity in the habitat due to the reallocation of resources between ramets (Pennings and Callaway, 2000). The loss of genetic diversity is expected to be slower as genetic drift does not act as fast through prolonged generation times (Orive, 1993; Young et al., 1996). The negative consequence of prolonged clonal reproduction is sexual

extinction – locally less adapted clones will become outcompeted creating monoclonal patches (Eriksson, 1989) and reduced frequency of inter-clone pollinations will occur (Kunin, 1997). Moreover ancient forest plant species are known to have almost no persistent seed bank (Bekker et al., 1998; Honnay et al., 2002a; Thompson et al., 1998) with some few exceptions according to Verheyen *et al.* (2003). However, those seed banks usually consist of few seeds (< 50 seeds/m²) and low colonization rates - range between 0.2 – 1.25 m/year (Honnay et al., 2002a).

Plue *et al.* (2010) have shown that former land use, land use intensity and time since reforestation has a great impact on seed bank recovery – even 150 years after reforestation seed banks had not regained former diversity (Plue et al., 2010). Experimental studies indicate that recruitment of field layer plants is often limited by low seed availability (Ehrlén and Eriksson, 2000) and poor seed dispersal (Cain et al., 1998; Willson, 1993) and forest plants are therefore expected to have a low colonizing capacity. There are several studies indicating woodland species limitations for colonization of isolated secondary patches thereby pronouncing the importance of dispersal limitation in fragmented landscapes (Grashof-Bokdam and Geertsema, 1998; Hermy et al., 1999; Hermy and Stieperaere, 1981; Peterken and Game, 1984; Petersen, 1994; Rackham, 1980; Whitney and Foster, 1988).

Species distribution in changing landscape depends therefore on the amount and configuration of the suitable habitat, species-specific migration, colonization rate to suitable habitat patches and the local persistence (Jacquemyn et al., 2003). Jacquemyn *et al.* conclude that the distribution patterns of forest plant species are influenced both by local and regional factors and not only aspects of fragmentation but even temporal patterns of landscape change may have large effects on plant diversity. Species adapted to forest interiors show the greatest declines in the smallest fragments, suggesting that landscapes dominated by small fragments with less core area and increased edge length will support fewer forest specific species, mainly due to a loss of species adapted to the interior.

Changes in soil chemistry

In Europe, currently the total area of forest cover is actually rising as reforestation is ongoing and new forests are planted on agricultural land. After the Second World War mostly coniferous trees were planted, but since the 1980s also broad leaved species have been planted as a consequence of political frameworks and subsidies in several European countries (Stanturf and Madsen, 2002). Soil compositions of these land areas are strongly altered by cultivation practices (ploughing, packing of the soils by heavy machinery, fertilizing, use of herbicides etc.). Compton and Boone (2002) suggest that ploughing and amendments have more pronounced impact on soil organic matter and nutrients than forest clearance per se (Compton and Boone, 2000). In general, the results suggest the following order of decreasing importance for plant ecology: Distance from the borderline > Soil reaction > Soil nitrogen > Soil moisture > Canopy cover (Brunet et al., 2000). Falkengren-Grerup *et al.* (2006) have studied land use effects on reforested soils and found that soil carbon was higher and pH lower in soils that had been forested continuously compared to soils that previously had been cultivated fields (Falkengren-Grerup et al., 2006). On recently afforested agricultural soils large amounts of carbon are bound into biomass and forest floor, sealed in trees and vegetation (Hooker and Compton, 2003), while in older continuously forested areas, carbon levels found in soils were much higher than in recent forests.

The success of future reforestation is directly dependent on soil conditions and vegetation response to secondary succession. Biomass production and even response to pollution, acidification and greenhouse gases may be influenced by nutrient availability caused by recent agricultural land use (Foster et al., 2003). Soil disturbance, even historical, may further increase the likelihood of the invasion of a community by invasive species changing natural species composition by outcompeting “true” forest species and threatening the ultimate goal of the reforestation – attempt to regain conditions resembling ancient forests (Hobbs and Huenneke, 1992).

Nitrogen

In general, nitrogen (N) is considered to be the most important nutrient for plants. Increased nitrogen levels in forests today, in particular on forest edges, mainly originate from agriculture, industry and transport. Since 1970s the use of nitrogenous fertilizers has increased considerably as agricultural production system sifted from extensive breeding on unfertilized pastures to cereal and oilseed rape cultivation. Even increase in average nitrogen indicator values have been demonstrated in central Europe forests during last decades (Diekmann and Falkengren-Grerup, 1998). Effects of nitrogen are in some cases found to be minimal as nitrogen is being used by cultivated crops and depleted from the fields by the time trees are planted while phosphorous is found in excess (Compton and Boone, 2000; Dupouey et al., 2002; Foster et al., 2003; Honnay et al., 1999; Verheyen et al., 1999).

VanBreemen and vanDijk (1998) have recorded an increase in the abundance of nitriophilous plants in Netherland forests, like *Galeopsis tetrahit* (vanBreemen and vanDijk, 1988). Other authors have reported a relative increase also in other plants related to high nitrogen content in the soil like *Rubus idaeus*, *Aegopodium podagraria*, *Epilobium montanum*, *Epilobium angustifolium*, *Sambucus* spp., *Stellaria media*, *Urtica dioica*, *Galeopsis tetrahit* and *Chamaenerium angustifolium* (Falkengren-Grerup, 1986; Thimonier et al., 1994). Kuhn *et al.* (1987) noticed a decline of *Rhytidiadelphus triquetrus* (a bryophyte indicating nutrient-deficient sites) due to enrichment of the sites with nitrogenous substances by comparing past and present floristic surveys in Switzerland (Diekmann and Falkengren-Grerup, 1998). Vascular plants have been identified that could in combination with for example Ellenberg values be used as indicators of nitrogen enrichment in soils (Falkengren-Grerup and Schottelndreier, 2004). A method for estimation of Ellenberg values as ecological indicator values for North European vegetation have been suggested (Diekmann, 1995; Diekmann, 1996; Persson, 1981).

pH

Forest edges in Europe surrounded by agricultural landscape often experience increased pH values as liming and fertilizing prevent soils under agricultural use from a pH drop and soil degradation (pedological leaching) typically following reforestation (Bossuyt et al., 1999; Huttli and Schaaf, 1995). Higher soil pH has been shown in herb-rich forests compared to moss rich

forests (Tamm and Hallbacken, 1988). Troedsson (1984) concluded that soil acidity was strongly affected even by tree species dominating in the area and the stand age. In growing forest soil acidity is increasing as protons are exchanged from plants for nutrients in the soil and by depositions like litter fall and acidic rain (Troedsson, 1984). Increased pH in the soil in turn can lead to lower rates of nitrification and higher nitrate leaching (Falkengren-Grerup and Diekmann, 2003; Honnay et al., 1999; Verheyen et al., 1999). Lower acidity in continuous forest stands can even be caused by different nitrification rates, leaching of nitrate and lime treating of agricultural land that has occurred in central Europe and Southern Sweden (Emanuelsson, 2002). Differences in pH rates and levels between recent and old stands are shown to be levelled out in 75 - 100 years after reforestation (Bossuyt et al., 1999; Koerner et al., 1997; Petersen, 1994; Wilson et al., 1997). Species that are associated with acidification of the environment are *Galeopsis tetrahit*, *Circaea lutetiana*, *Athyrium filix-femina* and particularly bryophytes such as *Dicranella heteromalla*, *Dicranum scoparium*

Brunet (2002, 2004) recorded higher abundance of acidifuge woodland species such as *Adoxa moschatellina*, *Mercurialis perennis* and *Circaea lutetiana* on reforested oak sites on former cultivated fields while on continuously forested land acido-tolerant species like *Maianthemum bifolium*, *Trientalis europaea* and *Gymnocarpium dryopteris* were more frequent (Brunet, 2004; Brunet et al., 2000).

Forest age and history

The age and history of the forest have been identified as one of the key factors explaining present vegetation composition (Brunet et al., 2000; Honnay et al., 1999; Jacquemyn et al., 2001) and species richness (Dumortier et al., 2002). Today most of the forested areas in Europe are relatively recent forests growing on former agricultural lands. Very few stands can be defined as ancient forests. These are normally found in areas that have been difficult to access (mountainous or wet areas) for agricultural purposes.

Homogenization of the soils and introduction of excess nutrients has taken place in such recent forests influencing present species composition. Old forests are crucial for threatened and

endangered species (Berg et al., 1994) and provide ecological services like storing immense amounts of carbon (Harmon et al., 1990; Pregitzer and Euskirchen, 2004). It has been indicated that the impact of historical land use on vegetation patterns is equal to or even larger than the effect of topography, soils, subsequent disturbance and current management regime (Flinn and Vellend, 2005; Motzkin et al., 1996) on the contrary to what was believed previously (McCollin, 1998). Jacquemyn *et al.* (2004) showed also changes to population genetics as higher genetic differentiation between populations and isolation by distance was found in older patches of fragmented landscape (Jacquemyn et al., 2004).

Agricultural land use and disturbance in general are expected to homogenize forest plant communities through environmental control of community composition – lower beta diversity is expected to occur in recent forests when agricultural fields are created by clearing forested areas initially occurring on larger environmental range, or when communities on a range of different soil types are converted into agricultural fields that are similar, leading to reduction of landscape scale variation in soil properties. Ross *et al.* (2002) confirms that is important to control for the age of fragments when species-area relationship is studied as anthropogenic disturbance in combination with fragmentation has been shown to have a stronger and more immediate effect on reducing native species richness and increasing exotic species richness compared to fragmentation alone (Ross et al., 2002).

Further studies

There is a considerable amount of theoretical knowledge available for forest edge effects on plant species diversity. Edge effects on plant species diversity and composition are expected to vary due to forest patch size, configuration and placement in the landscape. Ecological flows of energy, material and species between forest interior, edge and surrounding landscape and the effect of the flow of material on species composition and interactions between species have been studied on theoretical level. More empirical studies on species interactions and possibly comparing several factors and variables at the same time could shed some light on underlying mechanisms explaining observed and patterns. There is a need for further expansion of

knowledge in the field. It should be further studied and tested how information on edge responses can be used to improve the understanding of biodiversity at larger scales.

Ries and Sisk (2004) mention that the depth of edge influence is rarely quantified and the influence of multiple complex edge effects has been ignored. This is essential to really understand the impacts of fragmentation and other landscape-level changes. It is important to study how edges impact patch quality and how edge responses influence population and community dynamics. Hérault and Honnay (2005) recommend to distinguish species groups based on shared biological characteristics or species traits to investigate how local, regional and historical factors influence on the response patterns of vegetation to edge influence (Hérault and Honnay, 2005). Fox *et al.* (1997) divided species into four groups – core species, colonizers, weed species and pasture species and could show that weed species expressed the reverse pattern to core species. Plant functional trait analyses have previously been applied to studies of environmental changes (Bernhardt-Romermann *et al.*, 2008). Alinger (2011) finds it necessary to study the history and dynamics of the forest edges to be able to detect the effects of the factors that cause the differentiation of the boundaries (Alignier and Deconchat, 2011). Several researchers find grouping of species to be an effective method to study edge effects and further research in that field is needed.

Some studies have studied edge effects on species diversity at larger spatial scales, up to 1 km radius from study site, but further work in the field is needed. There are some new methods that have been tested but need further development. Gonzalez *et al.* (2010) used GIS tools to calculate and analyse the effects of forest edge on species richness. Whole woodlot, forest edge and forest interior areas were calculated using aerial photographs as cartographic support for the digitalisation of the boundaries of each woodlot. The area of the forest edge zone was obtained and subtracted from the area of the forest interior zone. This approach separating edge area from “true” interior area provides a new and more precise method to study processes and mechanisms operating in forest patches. Kumar *et al.* (2006) has developed a method to measure orientation of edges using DEM grid and surface analysis functions. Variables provided can be used to define the relative position of a location in two orthogonal aspect gradients (Gutierrez *et al.*, 2005). These new techniques give the possibility to use and develop new methods and to analyse patterns on larger landscape scale.

Edge effects have become more influential in present landscape due to land use changes that have induced changes in species diversity patterns. It is important to recognize the influence edge effects have on species composition. It is also important to distinguish between different edge types as they influence plant species differently and we need to pay attention to the distance of edge influence due to structural differences created by the forest and vegetation type. This distinction provides us with better tools to explain the patterns observed and possibilities to study mechanisms behind the patterns.

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