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Vascular plant species diversity in fragmented secondary plant communities: a landscape ecology approach

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Summary

Landscape ecology has been defined in a variety of different ways, but the common theme is the study of the ecological effects of ecosystem spatial patterning. Since the long history of landscape alteration has created novel systems with unknown dynamics, new tools are necessary to understand, manage and restore human dominated landscapes, preventing the loss of biodiversity. Among all, habitat fragmentation is the main process which affects biodiversity especially in human dominated landscapes.

This thesis is based on three research papers concerning the evaluation of plant species diversity in fragmented and secondary plant communities. Moreover, the effect of natural reforestation process on biodiversity of secondary plant communities was investigated through a review paper. Focusing in each paper on different specific objectives due to the variability of landscape context and habitat type, the overall goal of this work was to detect spatial and management components influencing vascular plant species diversity. Through the different tools and methodologies used in each case study, we want to demonstrate the great applicability and versatility of landscape ecology approach both in theory and practice.

The analyses were conducted on three fragmented secondary plant communities, i.e. meadow-pastures (Paper II), recent secondary woodlands (Paper III) and hedgerows (Paper IV), scattered in a dominant matrix type. Paper III was done during the collaboration with the Technische Universität of Berlin (Department of Ecology) during my research period abroad.

The case studies were conducted both at patch and at landscape level, considering actual field data and management variables of the secondary plant communities surveyed (patch level) and the analysis of landscape asset around (landscape level). The latter was performed by GIS analysis. Regression models were used to relate plant species diversity to spatial and management variables.

The survival of species depends on landscape dynamics and on spatial plant community configuration (Paper I). More specifically, where environmental site condition and management variables have not impact on secondary community variability and they did not differ between the surveyed communities, plant species diversity can be deeply influenced by spatial variables (Paper II and III). On the contrary, where management variables have a strong effect on secondary community alteration, i.e. in agrarian hedgerows, this effect is independent from the landscape assets of the different surveyed sites (Paper IV).

In general, the integrative methods used by the “landscape ecology approach” allowed us to quantify in a holistic way complex natural-cultural patterns and processes on different time-space scales that influenced vascular plant species diversity.

Riassunto

L'ecologia del paesaggio studia l'influenza dei *pattern* spaziali sui flussi di specie. La continua frammentazione ed alterazione delle fitocenosi in paesaggi antropizzati rende necessario comprendere le dinamiche delle comunità vegetali che caratterizzano il paesaggio antropizzato, cercando di evitare il più possibile la perdita di diversità biologica che spesso è conseguenza di tali trasformazioni.

La mia tesi è basata su tre articoli di ricerca riguardanti l'analisi della diversità della flora vascolare in fitocenosi secondarie e frammentate. In un lavoro di *review* invece, è stato analizzato l'effetto della riforestazione spontanea su fitocenosi secondarie a seguito dell'abbandono delle pratiche agricole. Ciascun lavoro è stato caratterizzato da specifici obiettivi, adattati in base alla variabilità del paesaggio e del tipo di fitocenosi secondaria indagata. Ciononostante, l'obiettivo comune di questa tesi è stato quello di esaminare l'influenza delle variabili di paesaggio e gestionali sulla variabilità della flora vascolare, tramite l'utilizzo di metodologie e strumenti propri dell'ecologia del paesaggio.

Le analisi sono state effettuate in tre fitocenosi secondarie e frammentate, i.e. pascoli (Paper II), neoformazioni boschive (Paper III) e siepi rurali (Paper IV), inserite all'interno di differenti matrici paesaggistiche. Il terzo caso di studio (Paper III) è stato sviluppato in collaborazione con la Technische Universität di Berlino durante il mio periodo di dottorato all'estero.

Le analisi sono state effettuate sia a livello di *patch* che di paesaggio, considerando quindi congiuntamente i rilievi floristici e le variabili gestionali (livello di patch) e l'analisi dell'assetto paesaggistico attorno alle fitocenosi indagate (livello di paesaggio). Le analisi di paesaggio sono state effettuate tramite strumenti GIS. Vari modelli di regressione sono stati utilizzati per mettere in relazione la diversità di specie vascolari con le variabili di paesaggio e gestionali.

La sopravvivenza delle specie dipende profondamente dalle dinamiche del paesaggio e dalla sua configurazione spaziale (Paper I). Più nello specifico, nei casi di studio in cui le variabili stazionali e gestionali sono ininfluenti o omogenee in tutti i siti, la diversità di specie vascolari è profondamente influenzata dalle variabili spaziali (Paper II e III). Dove invece la gestione altera sostanzialmente l'equilibrio della fitocenosi, l'effetto è indipendente dalle variabili di paesaggio (Paper IV).

In generale, i principi ed i metodi dell'ecologia del paesaggio che sono stati utilizzati nei casi di studio presentati, hanno permesso di quantificare precisamente i processi e le dinamiche che influenzano la diversità di specie vascolari a differenti scale spaziali e temporali.

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

- I. Sitzia T., Semenzato P., Trentanovi G. (2010) Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview. *Forest Ecology and Management*. 259 (8): 1354-1362
- II. Sitzia T., Trentanovi G. (2011) Maggengo meadows enclosed by forests in the Italian Alps: evidence of landscape legacy on plant diversity. *Biodiversity and Conservation*. 20 (5): 945-961
- III. Trentanovi G., von der Lippe M., Sitzia T., Ziechmann U., Kowarik I., Cierjacks A. (2011) Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. *Manuscript*
- IV. Sitzia T., Trentanovi G., Marini L., Cattaneo D., Semenzato P. (2011) Cultural system as determinant of hedgerow structure and woody species richness. *Landscape and Urban Planning*, *under review*

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1. Introduction

Landscape ecology has been defined in a variety of different ways (e.g. Forman and Godron, 1986; Burel and Baudry, 1999), but the common theme is the study of the ecological effects of ecosystem spatial patterning (Turner, 1989). Depending on the goals of each study, this effect is considered at different spatial and temporal scales (Risser, 1987). Moreover, it is evident that humans themselves and their activities are an integral part of the ecology of landscapes, and they should be treated as such in research (Wu and Hobbs, 2002).

Since the long history of landscape alteration has created novel systems with unknown dynamics, new tools are necessary to understand, manage and restore human dominated landscapes, preventing the loss of biodiversity (Farina and Morri, 2007). Thus, together with resource management, land use planning and other broad-scale environmental issues, landscape ecology is expected to provide a scientific basis for biodiversity conservation (Wu and Hobbs, 2002), clarifying the relationship between landscape pattern and ecological processes (Turner, 1989). Indeed, landscape can be defined by two strictly related components: **structure** and **function** (Figure 1). Landscape structure (or pattern) can be considered as the spatial relationship between landscape elements or patches, while landscape function (or process) is the interaction between these spatial elements (Hobbs, 1997). Finally, **landscape change** is the alteration in structure and function occurring through time.

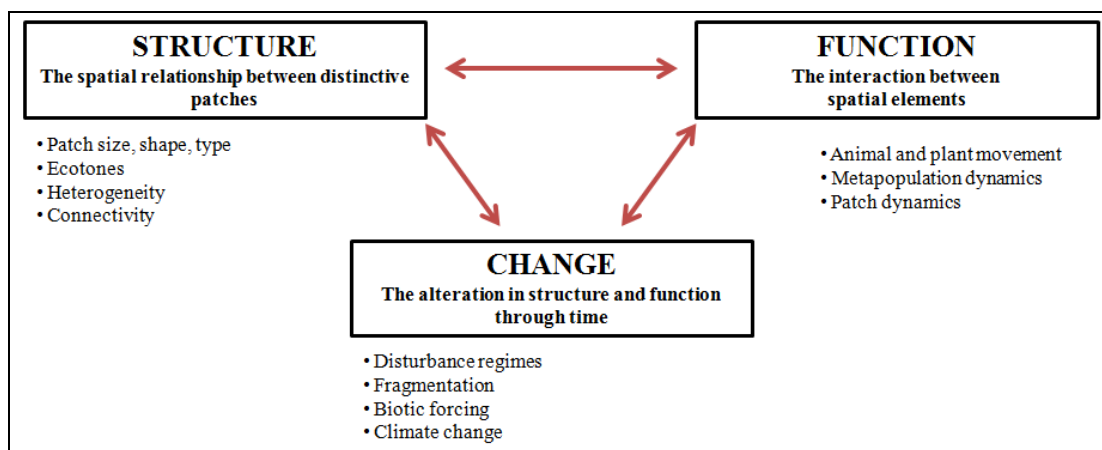


Figure 1: landscape ecology key components and their main study objectives. From Hobbs (1997), modified.

1.1 Fragmentation and secondary plant communities

The common topology of landscape in terms of patch, corridor and matrix (Figure 2) reflects the highly anthropocentric view of the world (McIntyre and Hobbs, 1999).

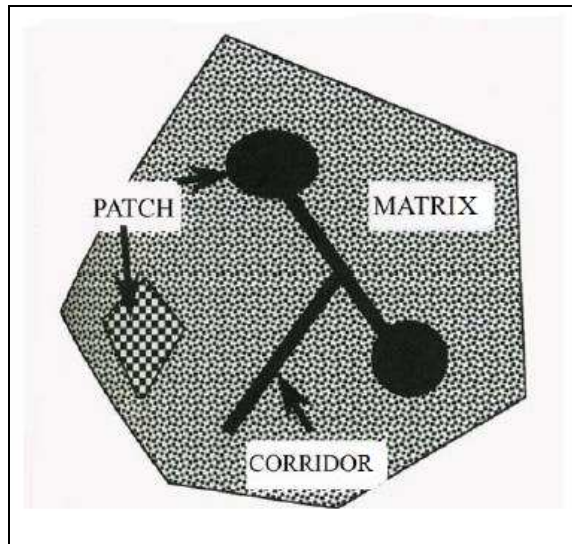


Figure 2: Landscape main elements: patch, corridor and matrix. From Burel and Baudry (1999), modified

This landscape classification reflects the high fragmentation of most of the habitats, from the natural to the most disturbed one's. Fragmentation was often used in the general sense of land transformation that includes the breaking of a large habitat into smaller pieces (Harris, 1984; Forman, 1995). In a different sense, this concept should be strictly related to the concept of habitat loss and/or isolation (Wilcove *et al.*, 1986). As reported by Forman (1995), habitat loss can take place with or without fragmentation as well as isolation that can increase with or without fragmentation. Based on these considerations, in our meaning **we refer to fragmented habitats to his strict ecological meaning, i.e. relatively small parcels of a habitat that differs from its surrounding matrix** (Forman, 1995).

Especially in the most industrialized regions, actual landscape patterns derived from centuries of human activities (Kirby and Watkins, 1998). The result is a mixture of natural and human-managed patches that vary in size, shape, and arrangement (Turner, 1989; Laforteza *et al.*, 2008). Levels of landscape alteration caused by human activities has been classified by many authors (e.g. Hobbs and Hopkins, 1990; McIntyre *et al.*, 1996). The cited studies help to better understand the continuum of human effects in term of exogenous disturbances on the habitat investigated (McIntyre and Hobbs, 1999). Indeed, disturbance is an important agent shaping and

controlling species diversity, and promoting system renewal (Pickett *et al.*, 1989). Secondary plant communities are the result of exogenous disturbance and they played an important role in preserving biodiversity (Peterken and Francis, 1999; Aude *et al.*, 2004; Weiss *et al.*, 2005). **This concept could be attributed to several “secondary plant communities” (also called in the text “secondary habitats”) including a broad range of different habitats, from pastures (e.g. Ludwig *et al.*, 2009) to more linear ones, like hedgerows (e.g. Backes, 2001).**

1.2 Secondary communities in changing landscapes. Effects on species diversity

During the last decades, we can observe two distinct phenomena: agricultural intensification (Tilman *et al.*, 2001; Robinson and Sutherland, 2002) of agronomically important areas of Europe (e.g. Robinson and Sutherland, 2002; Isselstein, 2003), and the abandonment of less productive and marginal agricultural land (e.g. MacDonald *et al.*, 2000; Lee *et al.*, 2002; Gellrich *et al.*, 2007; Sitzia, 2009) particularly on hills and mountain areas. As well as rural areas, the process of land abandonment involves also former industrial brown fields in post socialist countries (e.g. Kowarik, 2005).

Both trends have several consequences on biodiversity conservation at global scale (Tschardtke *et al.*, 2005; Rey Benayas *et al.*, 2007).

Agricultural intensification

Agriculture intensification is a well known phenomenon that convert more complex semi-natural ecosystems to simplified managed ecosystems through the intensification of resource use, on local and landscape scale (Tivy, 1990; Swift and Anderson, 1993; Vandermeer *et al.*, 1998; Hole *et al.*, 2005). On landscape scale, fields have been amalgamated and enlarged to enhance farming activity, fragmenting or destroying remaining semi-natural habitats (Tschardtke *et al.*, 2005) (Figure 3).

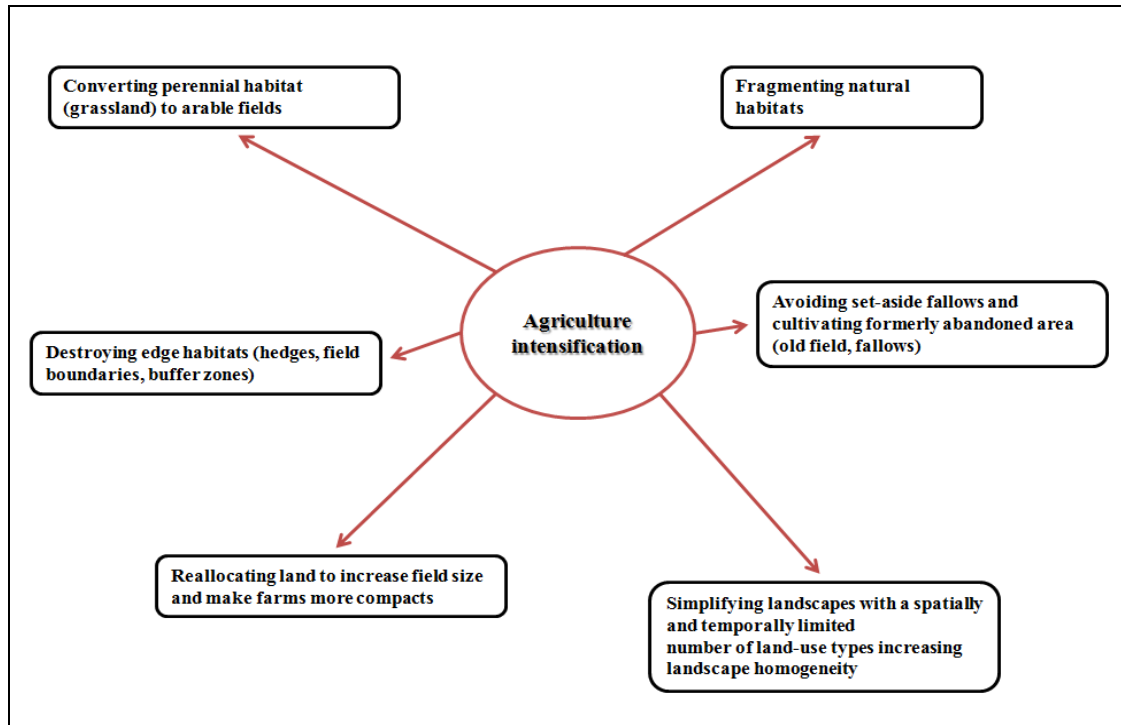


Figure 3: Practices of agricultural intensification at landscape scale. Adapted from Tschardt et al. (2005)

These practices represent the major cause of extinction of fragmented, small and isolated populations, like invertebrates (e.g. Cowley *et al.*, 1999; Kromp, 1999), birds (e.g. Donald *et al.*, 2001; Benton *et al.*, 2002), and plant species (e.g. Stewart *et al.*, 1994; Andreasen *et al.*, 1996).

Land abandonment

Increased farmland and agricultural intensification in productive lands occur alongside with farmland abandonment (Busch, 2006), especially in hilly and mountain areas (see Rey Benayas *et al.*, 2007; Tasser *et al.*, 2007). After land abandonment, vegetation succession occurs at varying rates depending on the site conditions. In areas below the alpine zone, this process results in dense shrub cover and finally in reforestation (Tasser and Tappeiner, 2002). The main drivers involved in this process are reported in Figure 4.

Natural reforestation is a major driver of changes in biodiversity patterns, but indicating and interpreting these changes is problematic because neither the processes involved nor the evaluation of impacts on environmental values are well understood (Cernusca *et al.*, 1996; MacDonald *et al.*, 2000). Many authors reported that natural reforestation leads to a loss of the

patchy land mosaic which is often linked to a loss of biodiversity (e.g. Burel and Baudry, 1995; Lindborg and Eriksson, 2004; Verhulst *et al.*, 2004). Moreover species composition of secondary forests can differ deeply from the previous forest, with several consequences on species diversity (e.g. Sitzia, 2009).

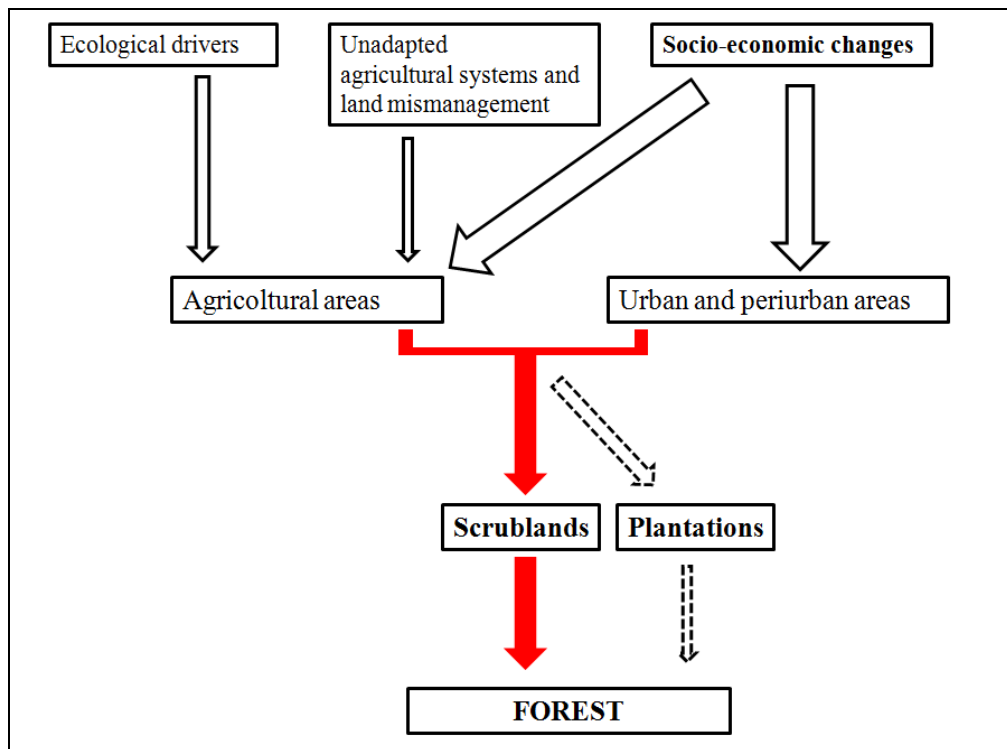


Figure 4: Natural reforestation drivers in abandoned lands

As we said before, land abandonment process involved also post-industrial sites of Europe, where “urban-industrial woodlands” (*sensu* Kowarik, 2005) emerged as well as in the former agricultural lands. These woodlands growth on different types of sites, such as rubble of former buildings (Kohler and Sukopp, 1964), rail yards that have fallen into neglect (Kowarik and Langer, 1994) and former iron, steel industries and mining areas (Weiss *et al.*, 2005). As well as managed or disturbed habitats they can be considered secondary communities too, due to its compositional distance from the former pristine vegetation before human settlements (Kowarik and Langer, 1994). Notably, some ecological processes, such as invasion of nonnative species, may be more prevalent in urban environments than in more natural ones (Spence and Spence, 1988; Trepl, 1995; Blair, 2001). Regarding plant species diversity, understanding the

behavior of alien species in cities is of crucial importance, since the cities serve as immigration sources (Sukopp and Werner, 1983) from which the aliens can spread further into the landscape. Particularly, non native species play a significant role in the colonization of derelict sites (Kowarik, 2005)

1.3 Landscape ecology in theory and practice: patch and landscape level approach

Due to the spatial heterogeneity of the landscapes, structure, function and change of landscapes are themselves scale-dependent (Turner, 1989). Since within a landscape several attributes tend to be similar and repeated across the whole area, a landscape manifests an ecological unity throughout its area (Forman, 1995). Thus, a repeated cluster of spatial elements characterize a landscape.

Individual patches and corridors can be considered as *local ecosystems* (sensu Forman, 1995) or *ecological units* inside a specific type of landscape, i.e. urban, rural ecc.. These elements of a landscape are sufficiently uniform to be considered an ecologically homogeneous, contiguous and uniformly disturbed unit (Petraitis *et al.*, 1989) so that for management purposes several similar ecological units may be grouped together and treated similarly, like homogeneous forest stands in silvicultural plans (Lafortezza *et al.*, 2008; Sitzia, 2009; Li *et al.*, 2011).

Thus, landscape can be considered as mosaic where a cluster of local ecosystems is repeated in similar forms over a kilometers-wide area (Forman, 1995), as shown in Figure 5.

Patch-level characteristics include area, shape, plant species composition and structure of an ecological unit (Graham and Blake, 2001), while at landscape level, factors such as isolation and type of habitat in close proximity can affect occurrence or persistence of species within a patch (e.g. Opdam, 1990).

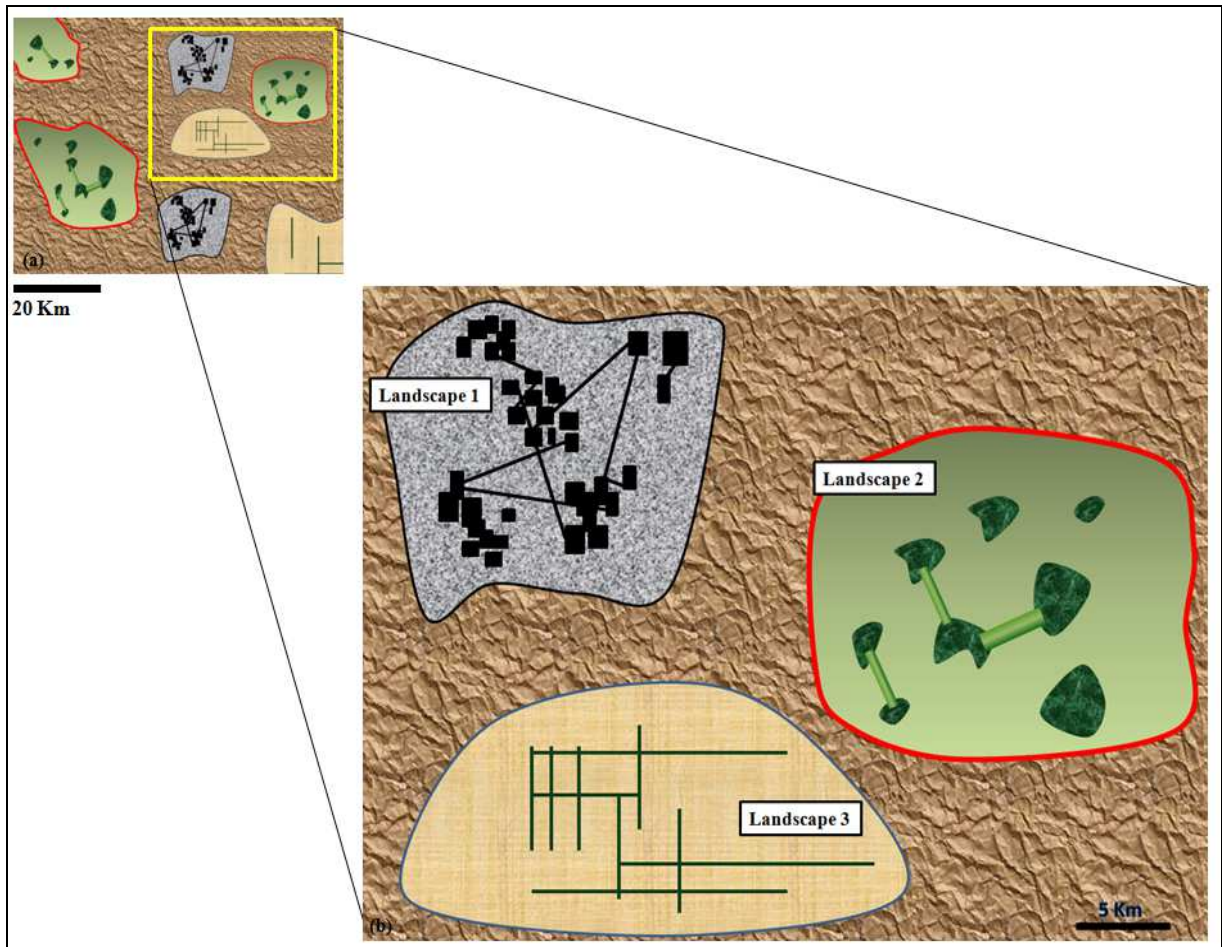


Figure 5: Representation of a simplified cluster of local ecosystems (b) repeated in similar forms at bigger scale (a). Landscape 1 could be associated with urban patterns; landscape 2 with forest-meadow patterns; landscape 3 with a hedgerow network in a crop matrix. In reality the local ecosystems are more nuanced and interpenetrating each other.

2. Structure, focus and goals of the thesis

The present thesis is based on three research papers (Paper II, III, IV) concerning the evaluation of plant species diversity in fragmented and secondary habitats (plant communities). The effect of natural reforestation process on biodiversity of secondary habitats was also investigated through a review (Paper I).

- I. Sitzia T., Semenzato P., Trentanovi G. (2010) Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview. *Forest Ecology and Management*. 259 (8): 1354-1362
- II. Sitzia T., Trentanovi G. (2011) Maggengo meadows enclosed by forests in the Italian Alps: evidence of landscape legacy on plant diversity. *Biodiversity and Conservation*. 20 (5): 945-961
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- IV. Sitzia T., Trentanovi G., Marini L., Cattaneo D., Semenzato P. (2011) Cultural system as determinant of hedgerow structure and woody species richness. *Landscape and Urban Planning*, *submitted manuscript*

Focusing in each paper on different specific objectives due to the variability of landscape context and habitat type, **the overall goal of this thesis was to detect spatial and management components influencing vascular plant species diversity**. All studies considered both the patch (with actual field data) and the landscape level (analyzing landscape characteristics that could influence plant species diversity dynamics inside the patch). Specifically we investigated:

- (a) if there are evidences on changing spatial patterns in rural mountain areas of the world in response to spontaneous reforestation and their possible implications on biodiversity (Paper I);
- (b) if the herbaceous plant richness and density of meadow-pasture patches is associated with current and historical landscape patterns in rural mountain areas (Paper II);
- (c) if black locust woodlands lead to homogenization of plant species richness in silver birch woodlands and the influence of urbanity and landscape patterns on this process (Paper III);
- (d) if tree species richness on hedgerows can be directly influenced by management, independently by other factors, such as landscape assets (Paper IV).

As Wu and Hobbs argued (2002), although some theories and methodologies exist, effectively integrating human-related processes into ecology may remain one of the ultimate challenges for ecologists. **Through the different tools and methodologies used in each case study, we wanted to demonstrate the great applicability and versatility of landscape ecology approach both in theory and practice.**

The following parts of the thesis contain a resume of the methodologies and results for each case study; within brackets the paper we refer for insights and deeper explanations.

3. Methods

3.1 Study areas

The research studies were conducted in northern-east Italy, i.e. in the Trento province (Paper II) and Veneto plain (Paper IV), and Germany, in Berlin urban area (Paper III), as shown in Figure 6. The review paper was done selecting research works conducted on several rural mountain areas of the world (Paper I).

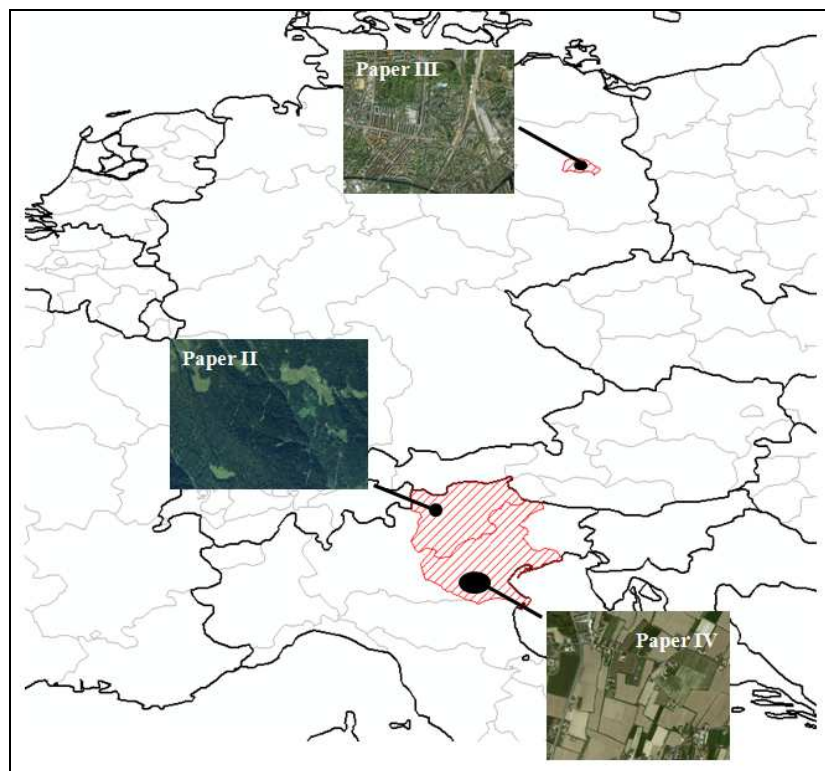


Figure 6: study areas of the research papers

The analyses were conducted on three fragmented secondary habitats, i.e. meadow-pastures (Paper II), recent secondary woodlands (Paper III) and hedgerows (Paper IV), scattered in a dominant matrix type (Table 1). Two of them are still managed (meadow-pastures and hedgerows), the other is completely left to spontaneous evolution (recent secondary woodlands).

<i>Paper</i>	<i>Secondary habitat</i>	<i>Matrix type</i>	<i>Management intensity</i>	<i>Type of paper</i>
I	Meadow-pasture and recent secondary woodlands	Woodland	Progressive abandonment	Review paper
II	Meadow-pasture	Woodland	Progressive abandonment	Research paper
III	Recent secondary woodlands	Urban	None	Research paper
IV	Hedgerows	Crops	Management	Research paper

Table 1: Resume of the papers composing the thesis

3.2 Data collection and elaboration

As reported in the § 2, the three research papers were conducted both at patch and at landscape level, considering actual field data of the secondary habitat surveyed (patch level) and the analysis of landscape asset around (landscape level) (Figure 7).

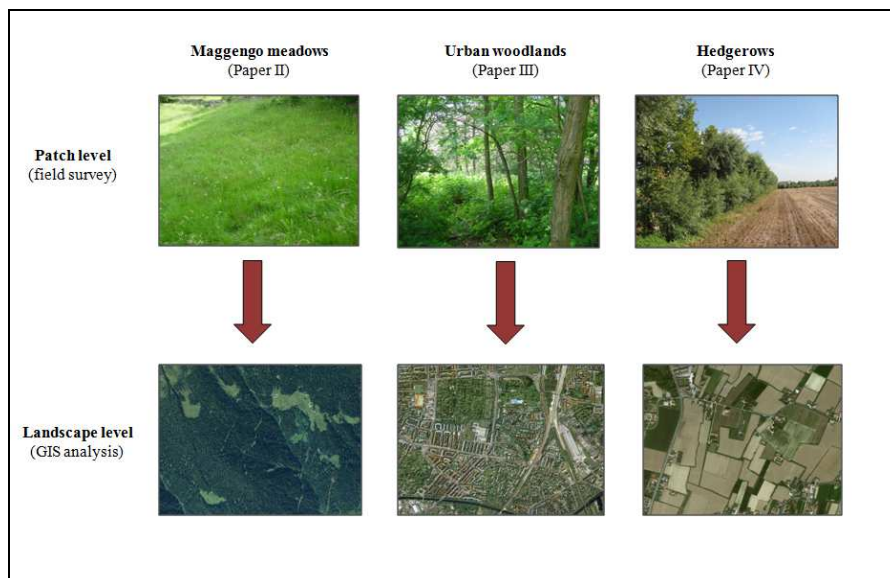


Figure 7: Patch and landscape level analysis of the surveyed habitats

3.2.1 Patch level analysis – vegetation data collection and elaboration

Despite their immobility, plants have several mechanisms that improve their ability to reach appropriate habitats and have evolved several attributes that allow them to function in a changing local environment (Bazzaz, 1991). It has been suggested that **plant diversity** should be important also in determining animal diversity (Hutchinson, 1959; May, 1990; Hunter and Price, 1992; Siemann *et al.*, 1998), thus plant species diversity is considered one of the best available **predictors of diversity of other taxa** (Pereira and Cooper, 2006). Moreover, the majority of plant species are relatively easy to identify through the help of few manuals. Thus, students and collaborators can help to reduce the sampling effort in a broad scale field survey, like those we made.

Within each study plot, all **vascular plant species were recorded**, except for hedgerows (Paper IV), where only tree and shrub species were considered. Species abundance was estimated using the **Braun-Blanquet method** in the woodlands patches (Paper III), while in meadow-pasture patches a **density index** was estimated through two or more transects in representative portions of the patch (Paper IV). Native and nonnative differentiation between species was used for hedgerows (Paper IV) and for woodland patches (Paper III). For meadow-pasture patches the shade-intolerant species were extrapolated, i.e. those threatened from natural reforestation process, from the total species number (Paper II).

We used several indices to measure plant species diversity, from alpha to beta diversity indices (Table 2).

Index	Type of diversity		Paper
	α	β	
<i>Species number</i>	x		IV; III; II
<i>Species density</i>	x		II
<i>Shannon</i>	x		III
<i>Simpson</i>	x		III
<i>Evenness</i>	x		III
<i>Jaccard</i>		x	III

Table 2: alpha and beta indices used in the papers

Alpha diversity is the within-habitat or intra community diversity (Whittaker, 1965; Peet, 1974), as shown in Figure 8. Among all, Shannon is the commonest index to quantify local species richness in small and ecologically homogeneous areas (Ricklefs and Schluter, 1993), while Simpson index is very suitable to underline compositional differences into a community (Lennon *et al.*, 2001). Species density is influenced by historical landscape configuration (Cousins and Eriksson, 2002) and land use history (Grace, 1999), thus we use this index to investigate biodiversity legacy with the historical landscape asset (Paper II).

Beta or between-habitat diversity is defined as the change in species composition along environmental gradients and it quantifies the spatial turnover or change in the identities of species (Whittaker, 1965; Koleff *et al.*, 2003). This latter is nowadays used in studies of **biotic homogenization** (Paper III) in urban areas, where native communities are gradually replaced by nonnative communities (McKinney and Lockwood, 1999). Among these indices, Jaccard distance is very suitable to detect ecological gradients (Faith *et al.*, 1987) in biotic homogenization studies (Olden and Rooney, 2006). Beta diversity value is calculated by the average pair-wise beta diversity index of each study plot compared to all other plots of the same group (Figure 8).

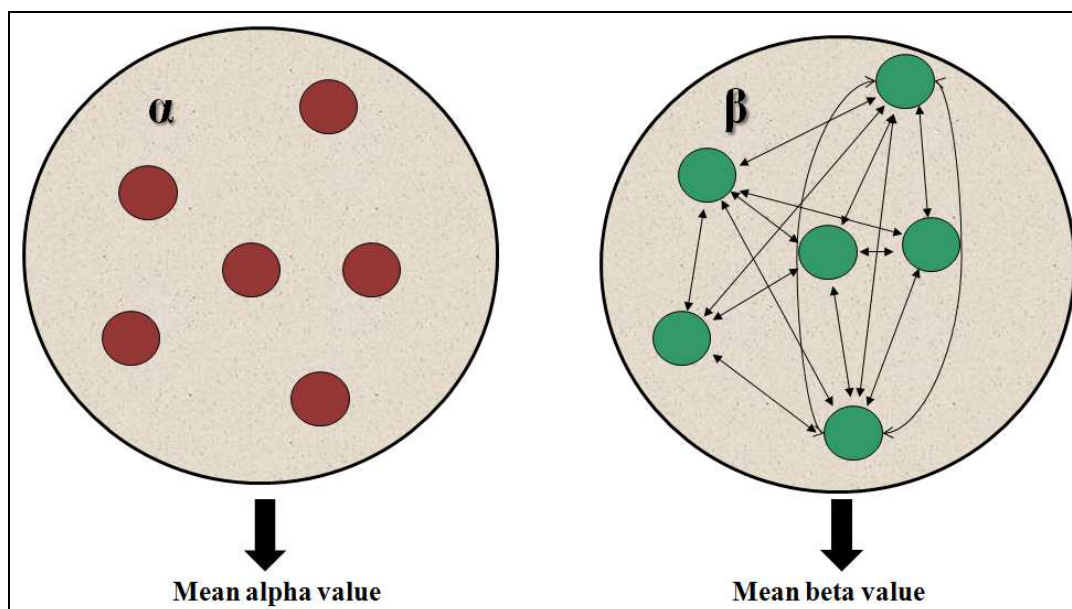


Figure 8: visual schematization of mean alpha and beta diversity calculation of six hypothetical plant communities. Mean alpha value is calculated simply through the arithmetical mean of alpha diversity values of each community samples (left picture). Beta diversity value is calculated by the average pair-wise beta diversity index of each community sample compared to all other communities of the same group (right picture).

Alpha and beta diversity indices were calculated through the free software package (*BiodiversityR*) developed within the R statistical environment, version 2.7.2 (R, 2005).

Management variables

Due to the intensive management regime of hedgerows in the Pò Plain, we added two variables strictly related with human management (in terms of logging activities and cutting regimes), i.e. basal area and **cultural systems**. These latter were classified according to the arrangement of plant growth forms as follows: multi-storied (shrubs, pollarded trees and coppice), high single-storied (pollarded trees and high trees or only pollarded trees or only high trees), low single-storied (shrubs and coppice or only coppice or only shrubs) and two-storied (pollarded trees and shrubs or pollarded trees and coppice or high trees and coppice). See figure below for some examples.

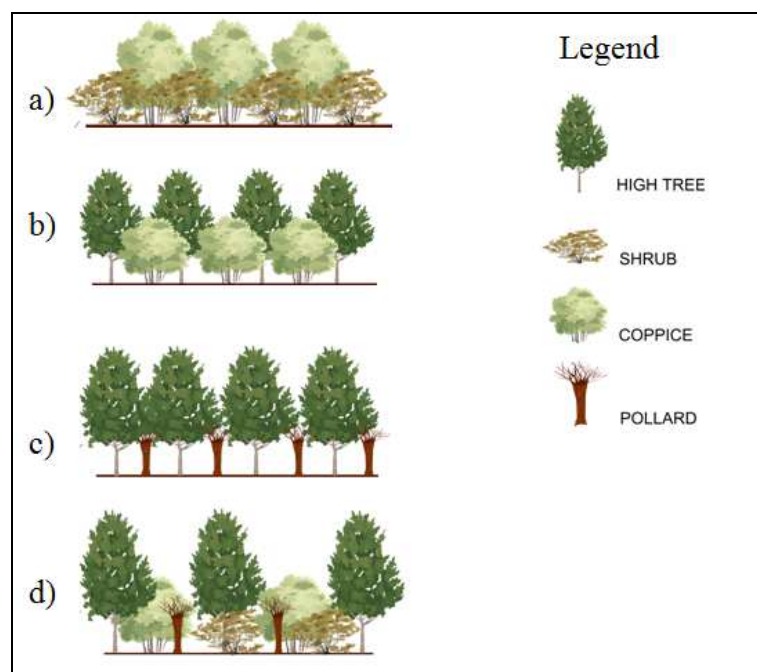


Figure 9: hedgerow's cultural systems examples: a) low single-storied; b) two-storied; c) high single-storied; d) multi-storied

3.2.2 Landscape level analysis – GIS analysis

The spatial patterning of ecosystems is a phenomenon that arises at the landscape level (Klopatek *et al.*, 1983). The ability to **quantify landscape structure** is prerequisite to the study of landscape function and change. For this reason, much emphasis has been placed on developing methods to quantify landscape structure (e.g. O'Neill *et al.*, 1988; Turner, 1990). Geographical information systems (GIS) of varying complexity have emerged as useful tools in addressing this kind of analysis (Turner, 1990).

The influence of landscape factors on plant species diversity was investigated differently in each research papers, **adapting GIS analysis** according to the specific characteristics of habitat, matrix type and human impact. For instance, **connectivity** was considered in all the four papers considered in this thesis. From a structural point of view, it can be defined as a measure of how connected or continuous a corridor, network or matrix is (Paper I). A complex index of **connectivity**, i.e. **Hanski index** (Hanski, 1994), was calculated between black locust patches (Paper III). This index takes into account the sizes and distances to all potential source populations (Figure 10) and has the best and most consistent performance for highly fragmented patterns of landscape (Moilanen and Nieminen, 2002), such as the Berlin urban area of the case study.

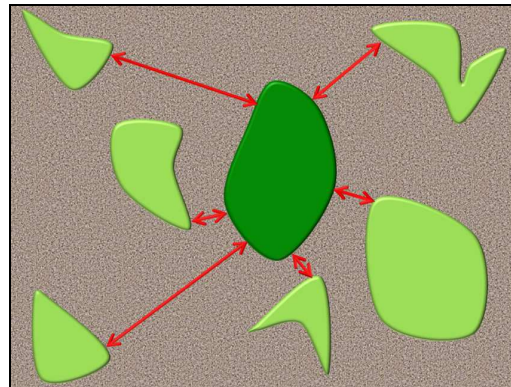


Figure 10: visual representation of hanski index principle: the calculation of isolation of the dark green patch takes into account both the distances from the possible source patches of the same habitat type around and the relative influence of their size

Instead, we used a simple measure of connectivity based on the **amount of habitat within a defined radius** (Wiegand *et al.*, 1999) in the more homogeneous and connected landscape of meadow patches in the Pejo valley (Paper II). Finally, in paper IV, we calculated

hedgerow **network density** (km/ha) as a structural connectivity index (Metzger and Dècamps, 1997) to characterize each agrarian landscape type surveyed in the Veneto plain (Figure 11).

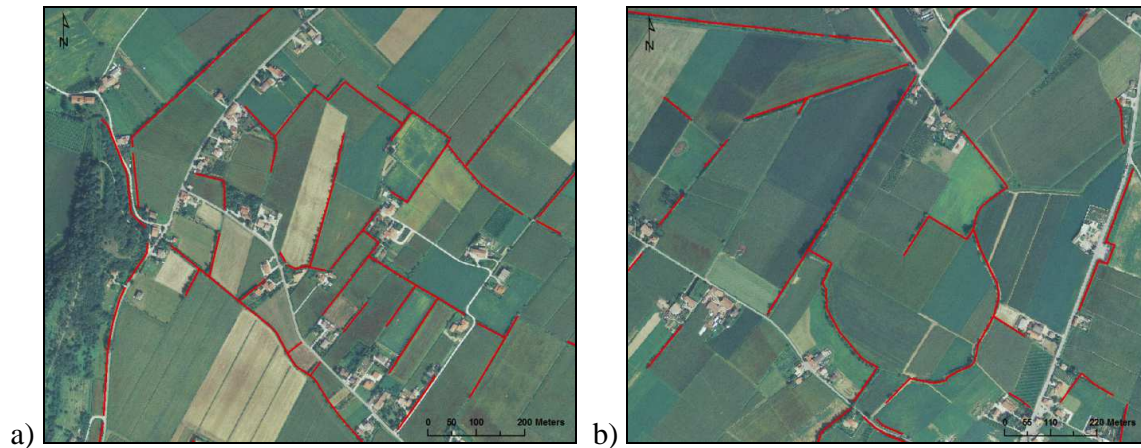


Figure 11: different hedgerow network density in the agrarian landscape of the Veneto plain (a) high hedgerow connectivity; (b) low hedgerow connectivity

As well as connectivity, patch spatial attributes can have strong effects on biodiversity (Forman, 1995). Among all, mean patch size (Paper I, II, IV), boundary length (Paper I) and several patch compaction and edge irregularity metrics (Paper II) were analyzed to determine their influence on plant species diversity (Table 3).

Landscape metrics	References	Paper
Patch (or corridor) size	(Forman, 1995)	I, II, IV
Number of patch	(Forman, 1995)	I
Patch compaction metrics		
Elongation index	(Davis, 1986)	II
Shape index	(McGarigal and Marks, 1995)	II
Fractal dimension index	(McGarigal and Marks, 1995)	II
Boundary length	(Forman, 1995)	I

Table 3: Landscape metrics adopted in the papers

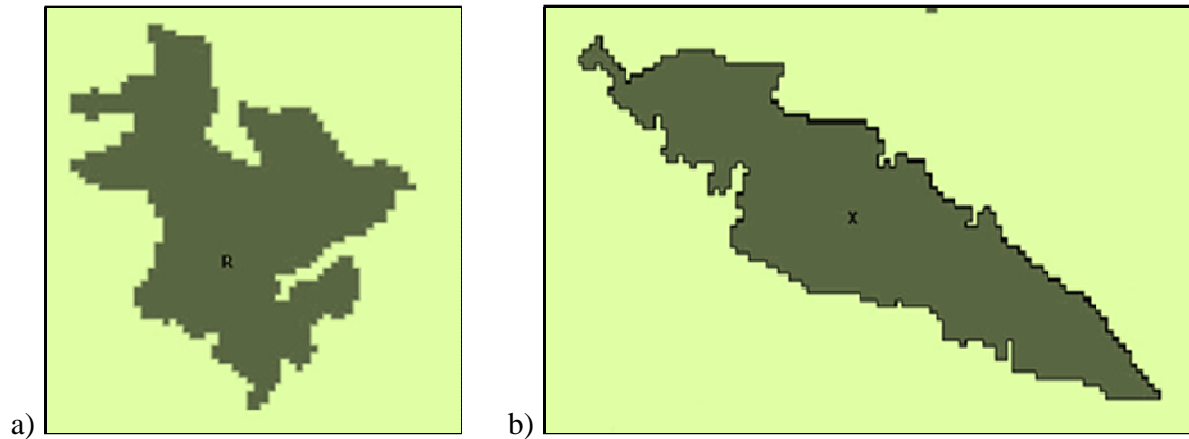


Figura 12: an example of different patch shape (a and b)

All the spatial analyses were made using the GIS software ESRI® ArcMap™ 9.2 (ESRI, 2006). Landscape metrics and land cover calculations were performed using PatchAnalyst (Rempel, 2008) in the GIS environment.

3.2.3 Statistical methods adopted

Landscape-level studies need methods to quantify spatial patterns and to determine relationships between functional process, biodiversity and landscape patterns (Turner and Gardner, 1991). The following part reports the main statistical methods and tests used in the research papers to determine differences between landscape and biodiversity patterns and to relate plant species diversity to spatial and management variables.

Testing differences between groups

We used several statistical tests to compare differences between group means (Table 4), depending on data distribution (parametric – non parametric tests) and on the number of groups sampled (two or more).

Besides the other well know and more classical procedures like ANOVA and t-test, **randomizations techniques** permit analysis of datasets that are not completely collected at random (Adams and Anthony, 1996; Legendre and Legendre, 1998; Strasser and Weber, 1999). Indeed, these kind of tests do not assume random sampling from well-defined populations, as more classical tests. Particularly in studies on the species turnover between communities through beta diversity indices (e.g. Legendre *et al.*, 2005; Ferrier *et al.*, 2007), this technique allows to

compare species diversity between spatially nested sampling (Paper III). The randomization procedure uses a reshuffling algorithm to place individuals in samples randomly while preserving the original species abundance and sample-size distributions (Crist *et al.*, 2003).

<i>Test type</i>	<i>Parametric</i>	<i>Non-parametric</i>	<i>Number of groups</i>	<i>Paper</i>
t-test	x		2	Paper III
Kruskall-Wallis Test		x	2 or more	Paper II
Mann-Whitney U Test		x	2	Paper III
Permutation (or randomization) tests		x	2 or more	Paper III
ANOVA	x		More than two	Paper II, IV

Table 4: Statistical tests adopted in the papers

Regression models

Ecologists frequently use models to detect and describe patterns, and regression models are often used as tools for quantifying the relationship between one variable and others upon which it depends (Elith *et al.*, 2008). More deeply, regression analysis is a statistical method used to investigate relations between a dependent variable, i.e. species richness, and predictors or independent variables, i.e. environmental and/or management variables, at a series of sites (ter Braak and Looman, 1987). In our three research papers, **the dependent variables are species diversity indices, e.g. alpha and beta indices, while the predictors (or independent variables) were mostly landscape and management variables.**

A common extension of simple linear regression is the case where we have recorded more than one explanatory variable. When all the predictor variables are continuous, the models are referred as multiple regression models (Quinn and Keough, 2002). Two main assumption of this kind of regression is that data could be normally distributed and explanatory variables cannot show any correlation and interaction effects with one other. **Correlation analysis** helps to

choose independent variables measuring the strength of association between them (Waite, 2000).

In the case study of paper II, species density was used as dependent variable, while historical size and connectivity of meadow patches as independent variables.

General linear mixed models (GLMMs) provide a more flexible approach for analyzing non-normal data when both **fixed and random effects** are present (Dormann *et al.*, 2007; Bolker *et al.*, 2008). An effect is considered "random" if the experimenter has not specifically chosen levels of the effect to be in the experiment, but has drawn a random sample from a larger population of possible level (Bennington and Thayne, 1994), i.e. our surveyed sites (Paper IV). A fixed effect is something that is repeatable. These effects are called "fixed" because the same levels of the effect would be used again if the experiment was repeated (Bennington and Thayne, 1994; Newman *et al.*, 1997). As reported by Bolker *et al.* (2008), "*GLMMs combine linear mixed models, which incorporate random effects, and generalized linear models, which handle non-normal data by using link functions and exponential family distributions*".

In the case study of paper IV, the number of woody species was used as dependent variable, while hedgerow area, cultural systems, tree basal area and site as independent variables. Site was treated as random factor.

The boosted regression tree (BRT) approach (Paper III) differs fundamentally from traditional regression methods that produce a single 'best' model. Indeed, BRT uses the technique of **boosting** to combine large numbers of relatively simple tree models adaptively to **optimize their predictive performance** (Elith *et al.*, 2006; Leathwick *et al.*, 2006). In the paper III, we used BRT both because of its predictive power and its flexibility in handling both categorical and metric response data.

Compared with conventional regression models, there are no *P* values to indicate the relative significance of model coefficients, degrees of freedom in the model are hard to determine, and the paradigm is quite different from one focusing on selecting a single 'best' model containing few parameters (Elith *et al.*, 2008).

Model selection in BRT, consistent with many modern techniques that focus on regularization through shrinkage (Hastie *et al.*, 2001), provides a coherent and robust alternative to traditional approaches such as stepwise variable selection (Whittingham *et al.*, 2006).

Although the lack of a single simple model may be regarded as disadvantageous from a traditional perspective, Elith *et al.* (2008) have demonstrated a range of methods for both interpretation and prediction, and these provide functional equivalence to many of the techniques used with conventional regression.

In the study (Paper III), mean Jaccard's distance was used as dependent variable (beta diversity index), while urbanity (i.e. proportion of built up area), proportion of railway habitats, connectivity index between black locust patches (calculated through the Hanski index), tree canopy cover and black locust invasion (categorical, black locust vs. betula plots) were included as predictors.

Multiple regression model was performed with the Statistica 9.0 software (Statsoft, 2009). All the other statistical analysis were conducted with R, version 2.7.2 (R, 2005). Permutation tests were performed through the coin package (Hothorn *et al.*, 2008). General linear mixed models were calculated through nlme package (Pinheiro *et al.*, 2010) while boosted regression trees with gbm package and additional scripts provided by Elith *et al.* (2008).

4. Main results and discussion

Regarding the analysis of plant species diversity in each surveyed community, we refer to the full papers reported in the appendix (§ 7).

The following results concern the **relationship between plant species diversity and landscape/management variables** analyzed through the regression models above explained (§ 3). They are just an extrapolation of the main results that we obtained in each case study (for deeper details see the Appendix).

4.1 Influence of landscape evolution on biodiversity (paper I) and plant species diversity (Paper II)

The review paper (Paper I) showed generically a negative effect of the shifting landscape mosaic following spontaneous reforestation on biodiversity. Among all, we can underlie the **general declining trend of scenic and grassland diversity values due to the loss of open spaces** (e.g. Motzkin *et al.*, 1999; Mazzoleni *et al.*, 2004; Lasanta-Martinez *et al.*, 2005; Leicht-Young *et al.*, 2007; Gellrich *et al.*, 2008; Kuemmerle *et al.*, 2008). Exception were reported by Laiolo *et al.* (2004) for alpine bird diversity.

The above mentioned results provided a good starting point to analyze more deeply the effect of spontaneous reforestation on semi-natural grassland plant species richness, through a research work on a specific alpine valley, as described below.

The research work in the Pejo valley (Paper II) has shown that ancient and current landscape patterns affected plant diversity. Throughout the years spanning from 1973-2006, patch interior species richness was positively correlated with patch size and more strongly with the current, while with shape index it was positively correlated only at 2006 (Table 5). Connectivity showed positive correlation only with species density (Table 6). The current patch interior species richness was not significantly correlated with any 1859 patch attributes, while species density was positively correlated with 1859 patch size, shape index and connectivity (Table 6).

Patch metrics		Years				
		1859	1973	1995	2000	2006
Patch size	<i>r</i>	0.066	0.321	0.289	0.274	0.322
	<i>p</i>	0.640	0.023*	0.041*	0.049*	0.022*
Shape index	<i>r</i>	0.098	0.140	0.264	0.218	0.362
	<i>p</i>	0.488	0.332	0.063	0.128	0.010*
Connectivity	<i>r</i>	0.213	0.088	0.157	0.190	0.162
	<i>p</i>	0.130	0.543	0.275	0.188	0.260

Table 5: Correlations of interior species richness with patch size, shape index and connectivity, throughout the years spanning from 1973-2006 and at 1859 (* < 0.05, ** < 0.01, *** p < 0.001; d.f.2006 = 57, d.f.1973-2000 = 56, d.f.1859 = 50)

Patch metrics		Years				
		1859	1973	1995	2000	2006
Patch size	<i>r</i>	0.470	0.112	-0.144	0.008	-0.033
	<i>p</i>	0.001**	0.437	0.318	0.958	0.982
Shape index	<i>r</i>	0.390	-0.085	-0.021	-0.017	0.086
	<i>p</i>	0.006**	0.559	0.883	0.007**	0.544
Connectivity	<i>r</i>	0.410	0.455	0.439	0.455	0.544
	<i>p</i>	0.003**	0.001**	0.001**	0.001**	0.000***

Table 6: Correlations of species density with patch size, shape index and connectivity, throughout the years spanning from 1973-2006 and at 1859 (* < 0.05, ** < 0.01, *** p < 0.001; d.f.2006 = 57, d.f.1973-2000 = 56, d.f.1859 = 50)

Our results show that the actual (2006) size and shape index tend to explain the variation in patch interior species richness among the remaining *maggengo* patches. This results were expected also from other studies (Forman, 1995; Cousins and Aggemyr, 2008).

Analyzing more deeply the effect of **historical (1859) landscape configuration on current plant species density**, we performed a multiple regression model including current species density as dependent variable and only two independent variables: 1859 size and connectivity. This explained 49% of variation in the current species density and showed that the importance of size was relatively higher than connectivity (Table 7).

Variable	b	β	<i>p</i>
Intercept	2.78	-	< 0.001
1859 size	0.23	0.43	0.009
1859 connectivity	0.89	0.36	0.025

Table 7: the multiple regression model for the effects of the 1859 size (log-transformed) and connectivity (arcsine transformed) ($n = 41$, $F(2,38) = 20.81$, adjusted $R^2 = 0.49$, $P < 0.001$) on the current species density (squared transformed). **b**: coefficients, **β** : adjusted coefficients.

Although patch interior species richness seems to be not influenced by the past and present connectivity, **this work shows that if the past landscape connectivity and patch size were higher than present, high values of present species density are sign that the influence of historical landscape configuration still exerts influence on plant diversity.** This result accords also to Cousins and Eriksson (2008). In order to support this latter result, we performed a literature research on species density in similar mountain landscapes. Compared to the few data we found (Stohlgren *et al.*, 1999; Fischer *et al.*, 2008), we can consider our species density values as being still high, demonstrating that the historical signal from the 1859 size and connectivity is still existent.

This study showed that changes in landscape pattern through long term dynamics could be one of the present plant species density determinants (Gustavsson *et al.*, 2007). Indeed, Pykala (2003) reported that species density was a more suitable indicator to evaluate spatial pattern changes effects on plant species diversity than species richness, which is generally more sensitive to environmental variables. Moreover, where environmental site condition and management variable aren't determinants of plant species diversity, a significant amount of variation in species data could be attributed to the pure effect of present spatial patterns.

4.2 Influence of landscape matrix and black locust invasion on homogenization of urban flora (Paper III)

The joint effect of *Robinia pseudoacacia* invasion, urban matrix components and canopy cover on beta diversity of *Robinia pseudoacacia* and *Betula pendula* plots was analyzed by using BRTs. The analyses revealed that *Robinia pseudoacacia* invasion had nearly no relative effect on the mean beta diversity of native species pools (Fig. 13a, b). In contrast, *Robinia pseudoacacia* invasion was the most important predictor for beta diversity in nonnative species (Fig. 14a,b). Mean beta diversity in the total and native species pools was strongly influenced by the proportion of built-up area around the plots with the highest beta diversity at low proportions and the lowest beta diversity at intermediate levels of building density.

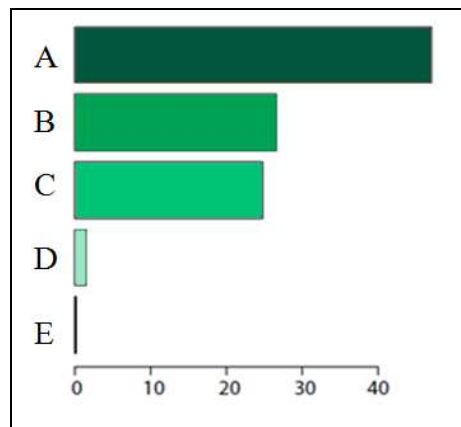


Figure 13a: relative variable importance plots for BRT analyses of the native species (cv correlation= 0.341, se= 0.117, explained deviance= 0.40). For the letters see below. The bar charts mean relative importance of the predictors for homogenization (i.e. Jaccard's dissimilarity); The longer the bar, the higher the influence of the predictor.

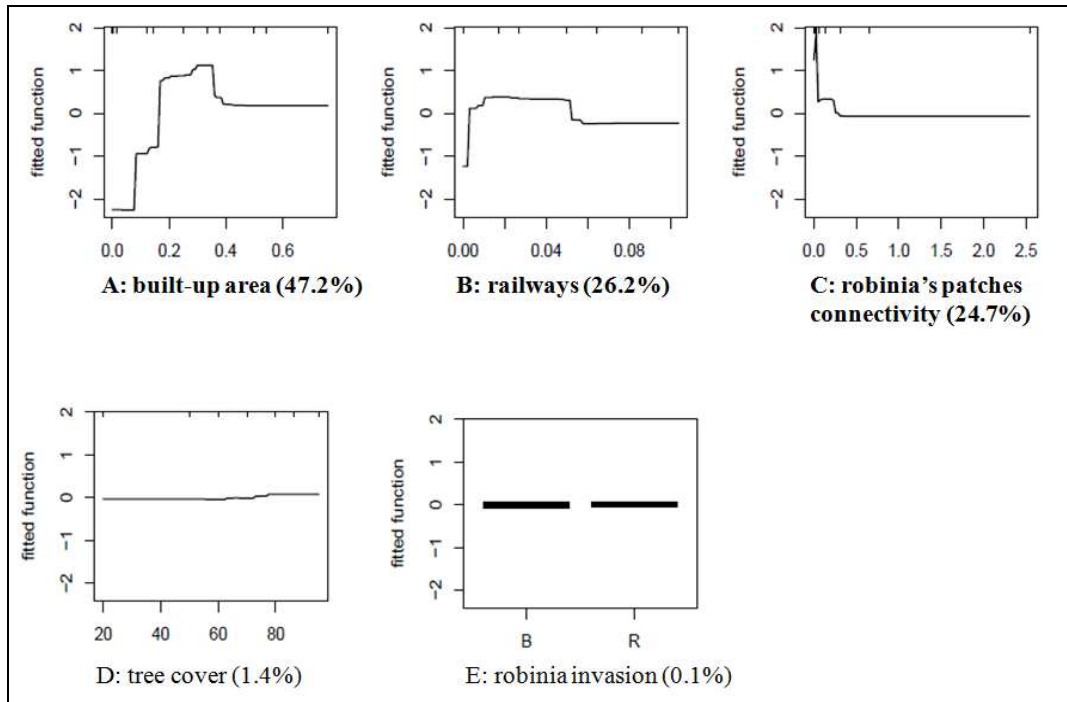


Figure 13b: partial dependency plots for BRT analyses of the native species (cv correlation= 0.341, se= 0.117, explained deviance= 0.40). The curves can be interpreted like regression lines where the dependent variable (Jaccard's dissimilarity) is on the y-axis, the predictor on the x-axis. In evidence the main factors affecting homogenization of nonnative species.

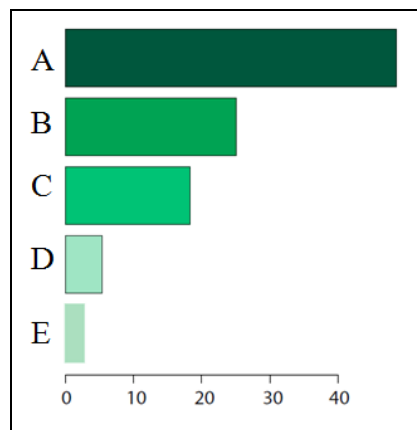


Figure 14a: relative importance plot for BRT analyses of the nonnative species (cv correlation = 0.34; se = 0.13, explained deviance: 0.24). For the letters see below. The bar charts mean relative importance of the predictors for homogenization (i.e. Jaccard's dissimilarity); The longer the bar, the higher the influence of the predictor.

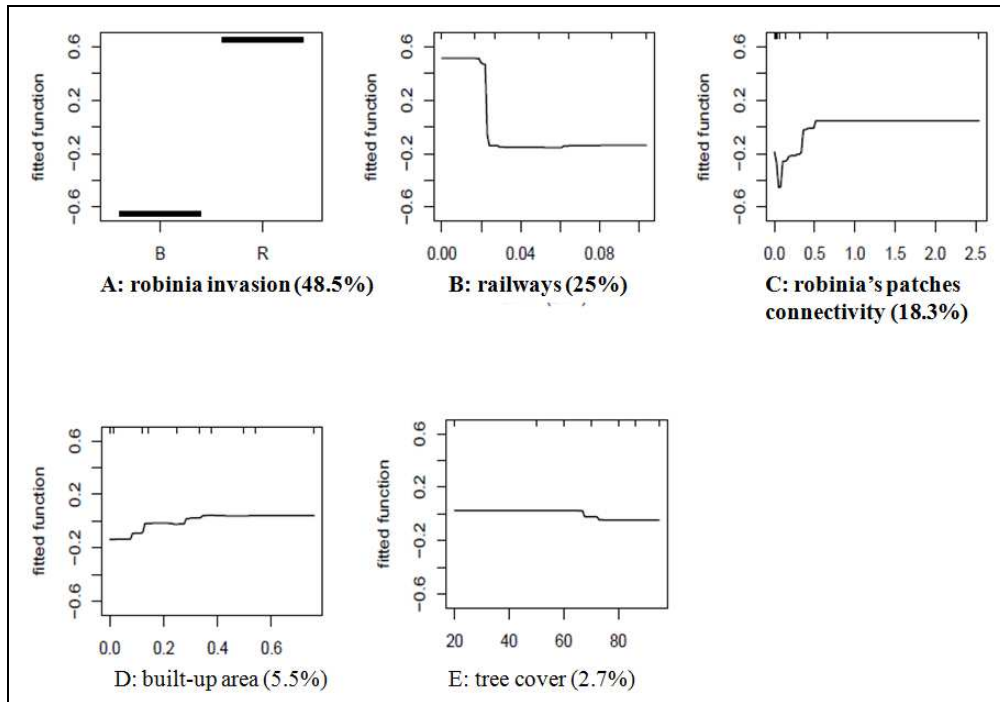


Figure 14b: partially dependency plots for BRT analyses of the nonnative species (cv correlation = 0.34; se = 0.13, explained deviance: 0.24). The curves can be interpreted like regression lines where the dependent variable (Jaccard dissimilarity) is on the y-axis, the predictor on the x-axis. In evidence the main factors affecting homogenization of nonnative species.

This study showed that biotic homogenization at the local level was increased by components of the urban matrix that promote woodland connectivity and species exchange. In accordance with the findings on the impact of urbanity on homogenization, the beta diversity of native species pools responded to the proportion of built up area. Indeed, BRT models of mean Jaccard's distance showed a strong impact of black locust invasion in the nonnative species pool whereas the beta diversity of native species responded exclusively to components of the urban matrix.

Our data provide evidence for varying mechanisms of homogenization of urban floras through plant invasions and urban matrix components at the local level. Plots invaded by black locust showed reduced beta diversity exclusively in the nonnative species pool despite a clear decrease in alpha diversity (see paper III). This can presumably be

attributed to the facilitation of archaeophytes in the course of nitrogen accumulation. Moreover, the proportion of built-up area led to homogenization of the native species pool. Connectivity of woodland patches and the proportion of railway habitats also contributed to a decrease in overall beta diversity through higher species exchange among woodland plots.

4.3 Influence of landscape patterns and management on plant species diversity (Paper IV)

Results of the mixed models (Table 8) showed a high significant effect of hedgerow area ($P < 0.001$) and cultural system ($P < 0.001$) on native woody species richness, as well as a marginal effect of basal area ($P = 0.034$).

	df	F	P
Log(Area)	1, 526	284.74	<0.001
Cultural systems	3, 526	38.358	<0.001
Log(basal area)	1, 526	4.518	0.034
Cultural systems x Log(Area)	-	-	-
Cultural systems x Basal area	-	-	-

Table 8: result from the general linear mixed models testing cultural system, hedgerow area, and basal area on native woody species richness in the seven sites. No interaction between the factors remained in the model. Site was included as a random factor.

Multi-storied support the highest number of species followed by two-storied hedgerows. High single-storied cultural system contains the lowest number of species (Figure 15).

Interaction between area and cultural system, as well as the interaction between basal area and cultural system, were not statistically significant. The slope of the curve between hedgerow area and native species richness was positive (Figure 16).

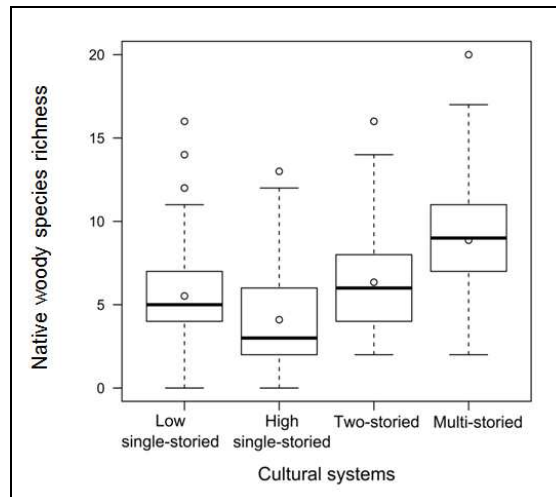


Figure 15: effect of the four cultural systems on native woody species richness. The dot indicates the mean while the solid line indicates the median.

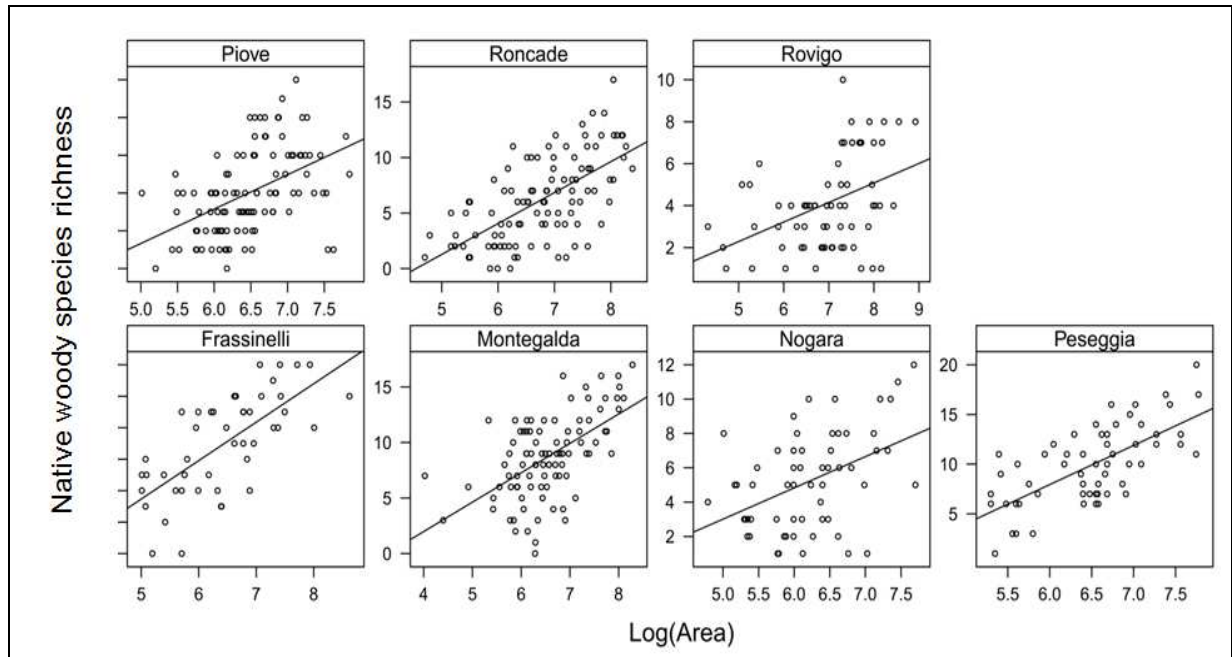


Figure 16: effect of hedgerow area on native woody species richness. Each plot represents one sampling site.

Each cultural system adopted in our study showed a relation with the various hedgerow structural characteristics. In addition, hedgerow cultural system, area and basal area exerted great influence on both structural features and native woody species richness. Both the effect of hedgerow area and tree basal area on woody species richness was not affected by hedgerow cultural system. Species accumulation with increasing area is a well know phenomenon also for hedgerows (Deckers *et al.*, 2004). Tree basal area is a correlate of stand volume and biomass, that we can interpret as saturation level (*sensu* Shorrocks and Sevenster, 1995).

This study indicates that the identification of cultural systems, gained from a visual estimation, may address native woody species richness across a wide range of hedgerow network densities and landscape types. The multi-storied hedgerows were those with the highest species richness and with the more complex structural attributes. Moreover hedgerow area is another key variable that has a strong influence on woody species richness.

5. General conclusions

Generically, the survival of species depends on landscape dynamics and on spatial habitat configuration (Paper I). More specifically, where environmental site conditions and management variables have not impact on secondary community variability and they did not differ between the surveyed communities, plant species diversity can be deeply influenced by spatial variables (Paper II and III). On the contrary, where **management variables** have a strong effect on the alteration of secondary communities, i.e. in agrarian hedgerow habitats, this effect is independent from the landscape assets of the different sites surveyed (Paper IV).

Moreover, the integrative methods used by the “**landscape ecology approach**” allowed us to quantify in a holistic ways complex natural and cultural patterns and process on different time-space scales (Naveh, 1994). Indeed, the three research papers combined vascular species diversity indices (alpha and beta diversity) with GIS landscape analysis (Paper II, III, IV). One of the the best way to find out relation between diversity indices and landscape variables (and management) are regression models. Among them, in the last years generalized linear mixed models (GLMMs) helped landscape ecologists to take into account for spatial autocorrelation of non-normal data that involve random effects (Paper IV). At the same time, boosted regression trees (BRT) combines regression trees algorithm with boosting technique, giving sometimes substantial predictive advantage over methods such as linear models (Paper III).

The **effect of isolation** is constantly an important factor influencing species dispersal between communities (Paper I). Both paper II and III showed the strong effect of the present connectivity on the secondary communities investigated. Moreover paper II showed that the past habitat connectivity could be one of the present plant species density determinants. However, in our research papers we considered connectivity between habitat patches (structural connectivity), not considering species’movement behavior in the landscape (functional connectivity). As suggested by Kindlmann and Burel (2008), a complete measure of connectivity should have both attributes to understand entirely the effects on landscape patterns on species diversity. Thus, further researchers could be addressed to analyze dispersion patterns of specific taxa of vascular plant species on the secondary habitats already investigated in this thesis.

These kind of studies have several implications in **landscape management and planning**. Studies like paper II could address conservation strategies to identify the most important (in term of surface, shape complexity and connectivity) meadow-pastures that should be preserved and managed in order to avoid the loss of shade-intolerant species, like those strictly related with this kind of habitat. Results like those of paper III help to understand the dynamics of nonnative species invasion and the role of new woodlands on urban plant species diversity. Since nowadays the importance of urban biodiversity is steadily growing for several ecological and sociological aspects (see Müller and Werner, 2010), urban planners have to take into account these aspects in planning and management of urban abandoned areas. Finally, agro-environmental schemes proposing hedgerow requalification and plantation derived from the institution of Agenda 2000 should include the hedgerow management practices suggested by our study (paper IV), because of their easily applicability in different landscape contexts.

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APPENDIX

Papers I-IV

PAPER I

Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview

Sitzia T., Semenzato P., Trentanovi G. (2010) Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: A global overview. *Forest Ecology and Management*. 259 (8): 1354-1362

1. Introduction

Few of the Earth's ecosystems remain undisturbed by anthropogenic activities (Brown, 1990; Sanderson et al., 2002; Foley et al., 2005), therefore the present landscape structure and function is the result of centuries of changes produced, not only by natural processes, but largely by human driving forces (Bürgi et al., 2004). Forests have particularly been the object of heavy and continuous human activities over a long period of time and, therefore, forest landscapes worldwide reflect, in their complexity, both ecological and socio-economical determinants (Piussi and Farrell, 2000).

For centuries many mountain and hillside areas have been the subject of deforestation to create space for agriculture and grazing, and forest cover was maintained and managed essentially for its timber and non-timber products and to prevent soil erosion and avalanches (Führer, 2000). However, the abandonment of traditional mountain agriculture has produced a natural forest recovery in many regions of the world (Walther, 1986; Kamada and Nakagoshi, 1997; Conti and Fagarazzi, 2004; Romero-Calcerrada and Perry, 2004), especially since the beginning of the last century. This phenomenon reflected the extensive depopulation and marginalization of rural mountain territories driven by socioeconomic factors such as immigration into urban areas (e.g., Rey Benayas et al., 2007).

The physical changes imposed on the landscape by the development of secondary woodland have brought both positive and negative consequences, depending on the geographical and economic context and on the scale of the sites. Such consequences include effects on fire susceptibility, water stocks and retention, soil stability and many others (Khanal and Watanabe, 2006; Bowen et al., 2007; Rey Benayas et al., 2007).

Among the ecological problems caused by natural reforestation, one of great interest is the reduction of open spaces resulting in a reduction of landscape heterogeneity and mosaic features, and frequently in a loss of cultural landscapes (Antrop, 1997; MacDonald et al., 2000; Nikodemus et al., 2005; Paci et al., 2006). The disappearance of patchy land mosaic is also often linked to a reduction in biodiversity (Hunziker, 1995; Cernusca et al., 1998; Burel and Baudry, 1999; Pedrini and Sergio, 2001; Lindborg and Eriksson, 2004; Verhulst et al., 2004). Secondary woodlands, in fact, often have lower levels of biodiversity than primary woodlands (Gerhardt and Foster, 2002); whereas low-intensity farming, which was typical of mountain regions, had produced over the centuries semi-natural habitats supporting a wide range of species (Beaufoy et al., 1994; Baldock et al., 1996).

Landscape metrics or indices are frequently used to assess the structural characteristics of the landscape and to monitor changes in land use (Turner et al., 2001; Van Eetvelde and Antrop, 2004).

The mosaic sequence, which is a series of spatial patterns over time, is the key to developing spatial models that can be directly compared ecologically (Forman, 1995). The survival of the species depends on landscape dynamics and on spatial habitat configuration (Fahrig, 1992; Hanski, 1994; Kleyer et al., 2007) which continuously change in quality, shape and spatial location.

A comprehensive review study about the changing spatial patterns due to natural forest recovery especially on rural mountain landscapes in the world seems to be lacking. We were able only to find a few review papers concerning, for example, spatial patterns and forest fauna (e.g., Bowen et al., 2007) or changing spatial patterns in northwest European landscapes (e.g., Kleyer et al., 2007).

In this paper we attempt to synthesize available evidence on changing spatial patterns in rural mountain areas of the world by identifying new landscape assets, and to provide a qualitative and quantitative synthesis of research findings regarding landscape modifications and their possible implications on biodiversity.

2. Review methodology and objectives

2.1 Definition of reforestation and spatial attributes

Within the context of this review, reforestation refers to the natural reestablishment of a forested landscape (by the regeneration of woody vegetation) on disused agricultural lands, meadows and pastures following farm abandonment (Forman, 1995) in regions where the potential natural vegetation (*sensu* Kowarik, 1987; Zerbe, 1998) is a forest. The reviewed papers often referred to reforestation as afforestation, forest expansion or forest recovery. The reviewed studies were not homogeneous in their definition of forest, so we accepted the definition of forest provided within each of the studies reviewed. Studies regarding planned reforestation and reforestation after natural or non-agricultural anthropogenic disturbance (e.g., selective logging or mining activities) were not considered (Bowen et al., 2007).

The focus of this paper is on changing landscape patterns. To describe such changes we considered three categories of spatial attributes of particular ecological significance as reported in Forman (1995): mean patch size (MPS), connectivity (CONN) and boundary length (BL). For each of the reviewed studies, the changes of these attributes were taken into account. Connectivity was considered, both structurally and functionally. In the second case, the target species of the case studies were considered. The shifting of the landscape mosaic over time was also analyzed recording the changes in patch number (NP). Each paper analyzed refers to changing spatial attributes of different land-use types, especially forests, meadows and pastures after natural reforestation. Moreover, we considered data on human settlements reported in the case studies to complete the analysis of landscape patch evolution.

2.2. Literature search and selection

We performed an electronic search in the Google Scholar (<http://scholar.google.it>) database of scientific literature using a combination of the following search strings in either the title or abstract of the reference study: “spatial pattern” and “natural reforestation” (or “afforestation” or “forest expansion” or “forest recovery”); “landscape” and “natural reforestation” (or “afforestation” or “forest expansion” or “forest recovery”); “landscape” and “land abandonment”; “patch size” (or “connectivity” or “boundary length”) and “natural reforestation”.

The search under the keywords: “mountain” and “natural reforestation” or “wildlife” and “natural reforestation” or “mosaic” (or “landscape pattern”) and “natural reforestation” provided very few references which did not follow our criteria. Supplementary articles were included from previous literature searches conducted by the authors. The review of 52 articles, identified through the search, is included in this paper. The selected articles met the following criteria: (i) the article must be published; (ii) the article must have data at least on one of the three spatial attributes considered, or on the number of patches

existing before and after the reforestation phenomenon; (iii) reforestation after land abandonment must be the main natural process investigated in the study. In Mazzoleni et al. (2004) we found a research study conducted in two study areas; so this review paper included the analysis of 53 case studies.

Using the information contained in each article, we recorded the geographic location, landscape composition and land-use types, forest expansion rate, time range of the research, surface and altitudinal range of the study area. Spatial attributes with their changes through time range were also recorded for each of the reviewed studies. Finally, we recorded the effects on biodiversity of spatial attributes changes (see Table 1 for further explanation of the data recorded).

Data type	Category	Explanation of terms
Forest expansion rate	-	Percent forest coverage growth in the study area through the time range considered
Time range	-	Length of reforestation process considered in years
Land use type	Forest	Follows the description of forest provided within each of the studies reviewed
	Open fields	Non forested patches such as meadows, pastures and croplands
	Human settlement	High density human-created structures
Spatial attributes	Patch	A relatively homogeneous non linear area that differs from its surroundings
	Boundary	A zone composed of the edges of adjacent ecosystems (or patches)
	Connectivity	A measure of how connected or continuous a corridor, network or matrix is from a structural or functional point of view
Biodiversity response	-	A brief summary of the responses of fauna or flora to the different changes of spatial patterns

Table 1- Explanation of data recorded for each of the studies reviewed.

3. The response of landscape spatial attributes to forest recovery

Most studies belonged to the temperate and continental Köppen–Geiger climate classification (Peel et al., 2007) and only one study, Olsson et al. (2000), considered polar climate area (Figs. 1 and 2). Only for 32 case studies accurate data was reported, both on forest expansion rate and time range analyzed in the study area (Table 2).

Most of the reviewed studies focused only on a portion of the spatial attributes that we were interested in (Table 3). Forty-nine case studies focused on changing mean patch size and 29 on changing number of patches. Twenty-two studies reported data on changing connectivity between patches and only sixteen on changing boundary length. Finally, thirteen case studies reported data on changing mean patch size of human settlement (Foster et al., 1998; Endress and China, 2001; Hall et al., 2002; Turner et al., 2003; Coelho-Silva et al., 2004; Mazzoleni et al., 2004; Shoshany et al., 2004; Acosta et al., 2005; Lasanta-Martinez et al., 2005; Mouillot et al., 2005; Baptista, 2008; Tappeiner et al., 2008; Václavik and Rogan, 2009).

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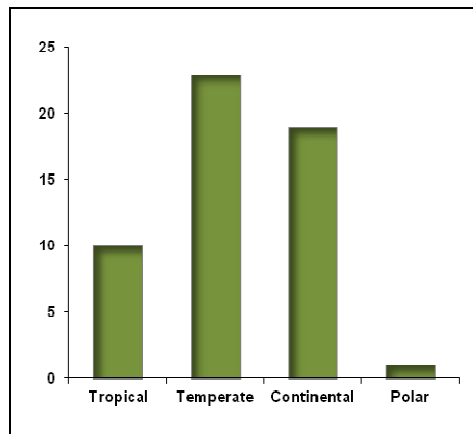


Fig. 1. Number of the reviewed studies in each of Köppen-Geiger climate classification areas.

Climate Classification Area	Nr. Case studies	Mean (conf. lim.)	
		Time Range	Reforestation rate/year
All	32	63.19 (± 18.49)	0.68 (± 0.35)
Tropical	5	37.8 (± 25.84)	1.37 (± 2.86)
Temperate	16	66.13 (± 31.47)	0.59 (± 0.3)
Continental	11	70.45 (± 32.58)	0.48 (± 0.24)

Table 2: Total mean and mean related to climatic zone (except for the polar one) and 95% confidence limits of time range and reforestation rate/year for the 32 case studies.

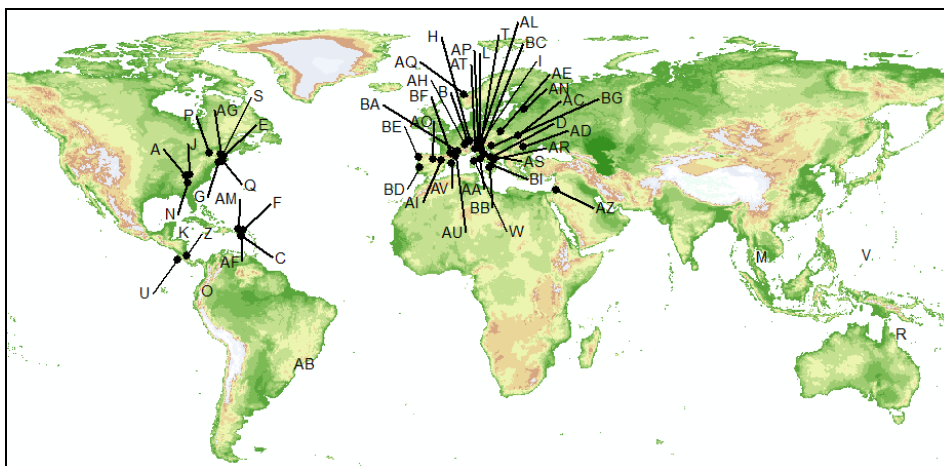


Figure 2- Geographic location of reviewed studies

Source	Altitudinal range (m a.s.l.)	Time range	Forest expansion rate	Spatial attributes investigated											
				MPS			CONN			BL			NP		
				F	OF	L	F	OF	L	F	OF	L	F	OF	L
Turner et al. (2003) [A]	650-1400	1950-1990	66%	+			+			-			+		
Bolliger et al. (2007) [B]		1979-1997	3%			//				-					//
Foster et al. (1999) [C]	100-1075	1936-1989	46%	-										+	
Van Gils et al. (2008) [D]	1000-1285	1975-2003	33.6%				+								
Foster et al. (1998) [E]	30-609	1830-1985	55%	+	-									-	
China et al. (2002) [F]	0-300	1936-1995	15%				+								
De Gasperis and Motzkin (2007) [G]	0-160	1830-2003		+	-										
Gellrich et al. (2008) [H]	600-2200	1950-2000	25%	+	-							-			
Tasser and Tappeiner (2002) [I]	1500-2300	1932-1998		+	-										
Tappeiner et al. (2008) [L]	660-3450	1865-2003	84%	+	-										
Bumrungsri et al. (2006) [M]	30-371	1980-2006					//								
Mitchell et al. (2002) [N]	600-1200	1900-2002		+			+			+					
Gunter et al. (2007) [O]	1900-2100	1964-2002		+	-		+	-		-				-	
Richards (1973) [P]		1948-1973		+	-					-					
Motzkin et al. (1999) [Q]	270-420	1937-1992	55%	+											
Florentine and Westbrooke (2004) [R]	700-800	1970-2003		+	-		+	-							
Leicht-Young et al. (2007) [S]	400-2200	1910-2007		+	-							-			
Niedrist et al. (2009) [T]	500-2000	1988-2008		+	-										
Wijdevan and Kuzee (2000) [U]	1100	1993-1995		+	-		+	-							
Endress and China et al. (2001) [V]	0-250	1947-1992	10.9%	+	-		+			+	-		-	-	
Helmer (2000) [Z]	1800-3700			+			+							-	
Hicks and Pearson (2003) [J]		1940-1998		+										+	
Aguilar (2003) [K]	1000-2849	1987-1998	60%	+	-		+			-				-	
Mouillot (2005) [W]	200-1100	1960-1990	13%	+	-		+								
Geri (2008) [AA]	300-1000	1933-2000	25%	+			+			+				-	
Baptista (2008) [AB]	0-1827	1970-2005	10%	+	-										
Kuemmerle et al. (2008) [AC]	200-1400	1986-2000	12.5%	+	-		+								
Kuemmerle et al. (2009) [AD]	100-2500	1990-2005		+	+									-	
Vaclavik and Rogan (2009) [AE]	200-800	1991-2001		+	-										
Aide et al. (1996) [AF]	10-440	1936-1995		+	-		//							//	
Hall et al. (2002) [AG]	0-1014	1880-2000	50%	+	-									//	
Laiolo et al. (2004) [AH]	1000-1900	1954-2002		+	-				-	+	-				
Lasanta-Martinez et al. (2005) [AI]	840-2566	1957-2000	42%	+	+					+	+		+	-	
Sitzia (2009) [AL]	70-2200	1973-2000	4.5%	+						+			+		
Lugo and Helmer (2004) [AM]	0-1338	1980-2001	1.2%		-		+						+		
Nikodemus et al. (2005) [AN]	0-300	1911-1990	18%	+	-								+	-	
Romero-Calcerrada and Perry (2004) [AO]	600-1300	1984-1999	13%				//								//
Tappeiner et al. (1999) [AP]	1600-2100	1920-1996	1%	+	-								+	+	
Olsson et al. (2000) [AQ]	200-1100	1960-1990	7%	+	-				-			-	+	-	+
Acosta et al. (2005) [AR]	291-906	1954-1992	8%	+	-								+	-	

Source	Altitudinal range (m a.s.l.)	Time range	Forest expansion rate	Spatial attributes investigated			
				MPS	CONN	BL	NP
Argenti et al. (2006) [AS]	650-1100	1955-1997	42%	+	-		+
Agnoletti (2007) [AT]	0-1850	1832-2000	54%		+		-
Preiss et al. (1997) [AU]	125-658	1978-1992		+	-		
Guirado et al. (2008) [AV]	115-485	1956-1993				+	+
Shoshany et al. (2004) [AZ]	100-400	1944-1990	40%	+	-	+	
Tatoni et al. (2004) [BA]	97-663	1890-1990	32%	+		+	+
Mazzoleni et al. (2004) [BB]	100-1050	1954-1984		+	-	+	-
Mazzoleni et al. (2004) [BI]	0-600	1955-1990		+	-	+	-
Torta (2004) [BC]	400-1100	1947-1993	10%	+		+	+
Coelho-Silva et al. (2004) [BD]	583-800	1947-1990	6.20%	+	-		+
Timoteo et al. (2004) [BE]	300-1300	1978-1994	4%	//	-	-	+
Metailiè and Paegelow (2004) [BF]	700-1200	1826-1995	20%	+	-		
Globevnik et al. (2004) [BG]	600-1028	1800-1995	52%	+	-		+

Table 3- Summary of time range, altitudinal range, forest expansion rate in the time range considered and changing spatial attributes analyzed in each case study. Spatial attribute changing: (+) Increased, (-) decreased, (//) unchanged and () data not available. (F) Forest, (OF) Open Field, (L) Landscape level.

The following sections report the responses of each spatial attribute to reforestation through time, for different spatial scales and land-use type (see Table 2 and Fig. 3 for a summary of landscape changing attributes considered in each case study).

3.1. Patch size

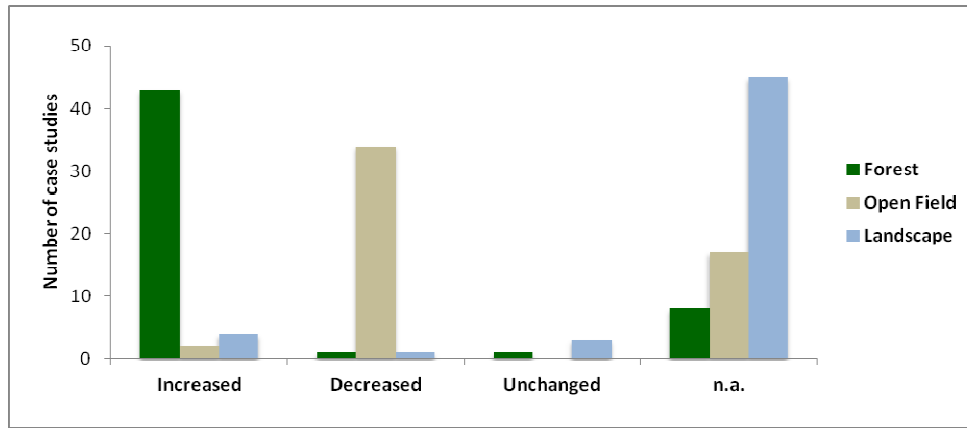
All selected case studies, except Foster et al. (1999) and Timoteo et al. (2004), showed an increase in forest mean patch size; this general trend was accompanied normally by a decrease in open field mean patch size, such as meadow or pasture. Only two studies found an increase in open field mean patch size (Lasanta-Martinez et al., 2005; Kuemmerle et al., 2009). At the landscape level, three studies documented no changes (Olsson et al., 2000; Romero-Calcerrada and Perry, 2004; Bolliger et al., 2007) and four studies (Mazzoleni et al., 2004; Shoshany et al., 2004; Agnoletti, 2007) showed an increase of this spatial attribute. Only Timoteo et al. (2004) found a decreasing trend. All of the case studies referring to changing mean patch size of human settlement reported an increase of this spatial attribute except Lasanta-Martinez et al. (2005) who found no changes in their study area.

3.2. Number of patches

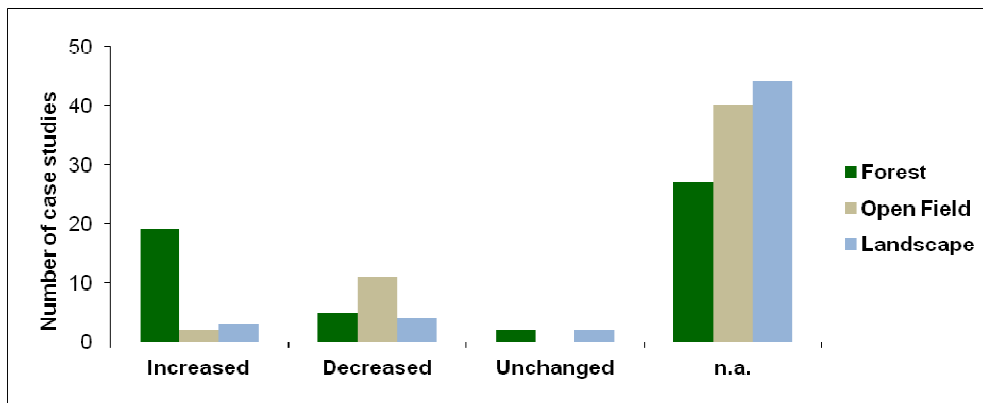
Nineteen of the 29 case studies that focused on the changing number of patches showed an increase in forest patch number, while 5 studies showed a decrease. Only Aide et al. (1996) and Hall et al. (2002) found no significant trends in the time range considered. Eleven case studies documented a contraction in the number of open fields. Nine case studies reported both the expansion in forest patch number and the contraction in the number of open fields (Olsson et al., 2000; Endress and Chinaea, 2001; Coelho-Silva et al., 2004; Mazzoleni et al., 2004; Acosta et al., 2005; Lasanta-Martinez et al., 2005; Nikodemus et al., 2005; Guirado et al., 2008). Only Tappeiner et al. (1999) and Globevnik et al. (2004) showed an increase in the number of open fields. At the landscape level, four studies (Mazzoleni et al., 2004; Tatoni et al., 2004; Agnoletti, 2007) showed a decrease in patch number, while just two papers (Timoteo et al., 2004; Torta,

2004) found an increasing trend. Finally Bolliger et al. (2007) and Romero-Calcerrada and Perry (2004) found no changes.

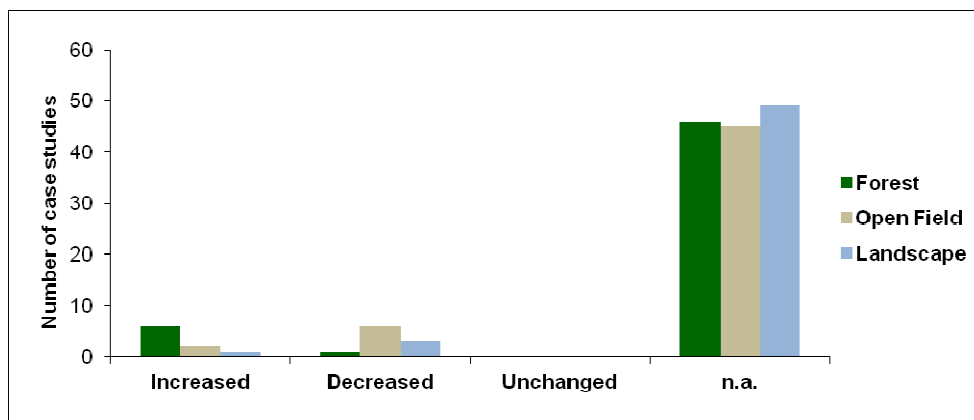
A)



B)



C)



D)

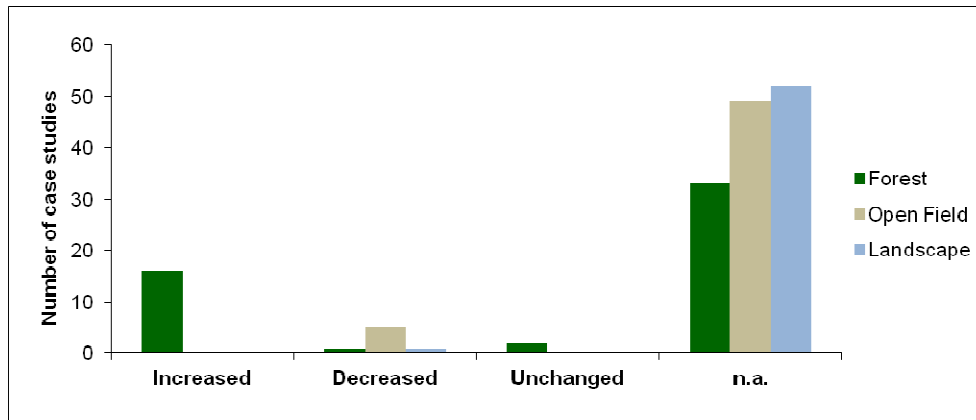


Fig. 3. Landscape changing attributes considered in the 53 case studies reviewed: (A) mean patch size (MPS); (B) number of patches (NP); (C) boundary length (BL); (D) connectivity (CONN).

3.3. Connectivity level

The majority of reviewed papers found an increase in connectivity between forest patches. Gunter et al. (2007), Florentine and Westbrooke (2004) and Wijdeven and Kuzee (2000) reported on a parallel negative trend in open field connectivity. Two case studies (Aide et al., 1996; Bumrungsri et al., 2006) found no changes in forest patches connectivity. Finally, at the landscape level, Bolliger et al. (2007) documented a lower connectivity. From a separate analysis of structural and functional connectivity (Table 4), we observed that ten case studies considered functional connectivity. The latter is species-specific, so each species has different responses to changing structural connectivity between patches (With, 1997). Mitchell et al. (2002) focused on the greater ant richness and abundance as a higher forest patches connectivity. In fact, this target group is the main plant seed-disperser in the study area. In Bolliger et al. (2007), seven open-land species were chosen to test the effect of the loss in habitat connectivity. Torta (2004) refers to the higher forest patch connectivity which allows an easier tree seed colonization of open fields. Olsson et al. (2000) refer to the vulnerability of grassland species to fragmentation of semi-natural grasslands.

Source	Type of connectivity			Biotic indicators	
	Structural	Functional	Plant species		Animal species
			Plant species	Animal species	
Turner et al. (2003) [A]	X				
Bolliger et al. (2007) [B]	X	X			<i>Alauda arvensis</i> , <i>Saxicola rubetra</i> (Aves); <i>Lacerta vivipara</i> (Reptilia); <i>Erebia aethiops</i> , <i>Melanargia galathea</i> , <i>Lysandra bellargus</i> (Lepidoptera); <i>Chorthippus scalaris</i> (Saltatoria)
Van Gils et al. (2008) [D]		X	<i>Fagus sylvatica</i>		
China (2002) [F]	X				
Bumrungsri et al. (2006) [M]		X	<i>Euphorbiaceae</i> ; <i>Moraceae</i> , <i>Lauraceae</i> , <i>Sterculiaceae</i>		

Source	Type of connectivity		Biotic indicators	
	Structural	Functional	Plant species	Animal species
			<i>Rubiaceae</i> species	
Mitchell et al. (2002) [N]		X		<i>Camponotus spp.</i> , <i>Aphaenogaster spp.</i>
Gunter et al. (2007) [O]	X			
Florentine & Westbrooke (2004) [R]	X			
Wijdeven & Kuzee (2000) [U]	X			
Endress & Chinaea (2001) [V]	X			
Helmer (2000) [Z]	X			
Aguilar (2003) [K]	X			
Mouillot (2005) [W]	X			
Geri et al. (2008) [AA]	X			
Kuemmerle et al. (2008) [AC]	X			
Aide et al. (1996) [AF]		X		<i>Dacryodes excelsa</i> , <i>Manilkara bidentata</i> <i>Sloanea berteriana</i>
Laiolo et al. (2004) [AH]	X			
Lugo & Helmer (2004) [AM]		X	<i>Spathodea campanulata</i> , <i>Guarea guidonia</i> , <i>Inga vera</i> , <i>Andira inermis</i> , <i>Tabebuia heterophylla</i> , <i>Syzygium jambos</i> , <i>Inga fagifolia</i>	
Olsson et al. (2000) [AQ]		X	<i>Primula scandinavica</i> , <i>Gentiana campestris</i> , <i>Gentiana amarella</i> , <i>Botrychium lunaria</i>	
Guirado et al. (2008) [AV]	X	X	<i>Quercus spp.</i>	
Tatoni et al. (2004) [BA]	X	X	<i>Quercus spp.</i> , <i>Pinus halepensis</i> , <i>Cedrus atlantica</i>	
Torta (2004) [BC]	X	X	<i>Quercus cerris</i> , <i>Acer campestre</i>	

Table 4 – Connectivity type and target species of each case study

3.4. Boundary length

Seven case studies showed a rise in forest boundary length; among these, two (Endress and Chinaea, 2001; Laiolo et al., 2004) also reported a contraction in open fields boundary length. Turner et al. (2003) found a decreasing trend for forest patches. At the landscape level, three studies (Olsson et al., 2000; Mazzoleni et al., 2004) report a decreasing trend of boundary length between patches, while Torta (2004) showed an increasing trend.

4. Biodiversity response

Understanding the processes of land-use changes in mountain regions is important because such changes are related to a variety of ecological and cultural consequences (Gellrich et al., 2007). With the analysis of changing spatial patterns, we can make an operational assumption, i.e., that the initial landscape mosaic is ecologically more suitable for a taxon or a functional group of species than the new landscape structure, or the contrary.

Among the many consequences of the shifting mosaic, some papers report, for example, the decline of scenic diversity and of grassland biodiversity values due to the loss of open spaces (Motzkin et al., 1999; Leicht-Young et al., 2007; Gellrich et al., 2008; Kuemmerle et al., 2008). In the Mediterranean region, Mazzoleni et al. (2004) reports on a dramatic shifting of floristic composition in both study areas and Timoteo et al. (2004) refers to the negative effects of landscape fragmentation on various target species that are unable to live in small patch habitats. Instead, Laiolo et al. (2004) referred to the positive effects of the increase in forest mean patch sizes on the diversity of alpine birds. At the landscape level, some authors report the negative effects on landscape cultural structure (Nikodemus et al., 2005; Agnoletti, 2007) and plant diversity (Lasanta-Martinez et al., 2005) due to the growth in the number of forest patches. van Gils et al. (2008) also reported a negative effect on landscape diversity due to the rise of forest patches connectivity. The increase in both number of forest and open fields patches made the Passeier Valley landscape more ecologically interesting for his new patchy property structure (Tappeiner et al., 1999). On the other hand, the same trend is negative for the patchwork structure in Norway (Olsson et al., 2000).

5. Synthesis and further research

Landscape heterogeneity was often maintained and supported by a complex social organization with strict rules as regards the management of resources (Fuentes, 1990; Gomez Sai et al., 1993; Kamada and Nakagoshi, 1997). A criterion on which to evaluate landscape change might be the increase in homogeneity or heterogeneity at various spatial scales (Di Pietro and Balent, 1997).

The analysis of spatial attributes showed a decreasing trend of semi-natural habitats such as meadows or pastures due to natural reforestation; the concentration of grazing in a few highly intensive areas resulted in livestock controlling the increase of vegetation in those sectors, while the rest of the land had been subjected to little pressure, having been left to a natural process of plant succession (Lasanta-Martinez et al., 2005). Two key variables in these processes are time range and the historical landscape pattern. Kozak et al. (2007) refers to the fact that in the Carpathians Mountain region a 15-year time period is likely to be too short for a full canopy to develop via natural reforestation. Moreover, Pausas (2003) showed the strong influence of the initial forest distribution on the pattern of forest expansion.

We cannot draw general conclusions on reforestation rates, mainly because, the study data referred to very different time spans in each climatic region. More homogeneous studies are recommended with respect to the time frames analyzed.

The socioeconomic phenomenon of human settlement development reported in some papers is related to the general suburbanization process, where the areas of low-density residential development is rapidly expanding as in Endress and Chinaea (2001), Václavik and Rogan (2009), Hall et al. (2002) and Shoshany et al. (2004). This trend is followed by an expansion of forest mean patch size. This phenomenon is not always related to the loss of open spaces due to agricultural abandonment, but also to the growth of building density below the forest canopy as reported in Turner et al. (2003), where many people live in homes constructed in the forests. The parallel increase in the extent and connectivity of major forest

communities and exurban development could indeed reduce some benefits of forest regrowth (Askins et al., 1990).

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PAPER II

Maggengo meadow patches enclosed by forests in the Italian Alps: evidence of landscape legacy on plant diversity

Sitzia T., Trentanovi G. (2011) Maggengo meadows enclosed by forests in the Italian Alps: evidence of landscape legacy on plant diversity. *Biodiversity and Conservation*. 20 (5): 945-961

1. Introduction

Among the consequences of land transformation and fragmentation, the loss of biodiversity is possibly one of the areas of greatest interest to ecologists (Forman 1995; Hobbs 1997; Moore et al. 2009; Ormerod 2003). Over the alpine mountain landscapes, the decline of agriculture and farming (Bozon and Grossi 1993; MacDonald et al. 2000; Meeus et al. 1990; Walther 1986) has produced the fragmentation of many semi-natural habitats suitable for grassland plant species (Baur et al. 2007; Da Ronch and Ziliotto 2008; Dullinger et al. 2003; Maurer et al. 2006; Spiegelberger et al. 2006). Semi-natural grassland habitats have resulted from the perforation of the primeval forests by human-made clearings. Subsequently, the most relevant type of human and natural driving forces has produced a mosaic sequence which is the current spatial pattern (Bürgi et al. 2004; Franklin and Forman 1987; MacNelly 1994; Sitzia et al. 2010). Small-patch landscapes (Forman 1990) with mountain meadows surrounded by a forested matrix is one of the typical spatial patterns of European alpine landscapes. Patch size and shape played a great role in conserving species diversity in similar landscapes (Forman 1995). However, their relationships with plant species diversity have been poorly investigated (e.g. Cousins and Aggemyr 2008), especially in terms of their historical perspective (Cousins et al. 2007). Further similar studies are necessary to promote restoration and conservation efforts (Kettle et al. 2000; Lindborg and Eriksson 2004a). They help identify spatial attributes that act as surrogate indicators of plant diversity of enclosed herbaceous patches (Cousins and Aggemyr 2008; Forman 1995; Moser et al. 2002). Such research should address not only the spatial effects on biodiversity, but also include a temporal dimension (Ernoul et al. 2006; Lunt and Spooner 2005). In fact, an actual vegetation pattern is considered to be a legacy of the historical landscape pattern (Helm et al. 2006). This is particularly true in the mountains of the European Alps where the spontaneous expansion of woodlands in old fields has been a common phenomenon in past decades (Feoli and Scimone 1982; Barbero and Quezel 1990; Falcucci et al. 2007; Tasser et al. 2007; Gellrich and Zimmermann 2007; Sitzia 2009; Gerard et al. 2010; Tattoni et al. 2011). Moreover, most of the surviving meadows and pastures are composed of systems of small patches, which are increasingly subject to total human abandonment (Grossi et al. 1995). Forest expansion causes the edge effects to extend progressively further from the border into the field interior or leads to outward radiations of colonization from established woody plants. The two processes may act alone or together, changing the minimum dynamic area (Pickett and Thompson 1978) and the disturbance regimes (Turner et al. 1993) and underlying many ecological processes that are superficially related to habitat area (Ewers et al. 2007).

The first aim of this study is to verify significant spatial pattern changes in the last decades. In fact, spatial trends through time have ecological effects in land mosaics (Forman 1995; Olsson et al. 2000; Li 2008). In particular, landscape spatial structure is an important factor for spatial process such as local dispersal (Borcard et al. 1992). Secondly, we focused our attention on the effect of spatial components and significant trends on grassland biodiversity in a homogeneous landscape as regards to environmental

variables and historical management regimes. Therefore, this study focused on the maggenghi, adopting their single patches as the units of observation, which consist of the whole maggengo meadows area.

Maggenghi are one of the most typical mid slope meadow of the European Alps, for centuries managed with traditional and low intensity techniques. The maggenghi belong to the Trisetion alliance, are generally mown once a year or even less frequently, and are fertilized only with manure. When necessary and possible, they are irrigated with furrows and the natural slope is reduced by dry-stone walling to create terraces, that function also as boundaries with forest, alone or in addition to timber fences (Albertini 1955; Pedrotti 1963). They are managed mechanically, and only the smallest are still mown manually, most of them being grazed by dairy cows and young cattle in the late and/or in the early summer (Niedrist et al. 2009).

We studied enclosed maggengo patches in a forested landscape of a Central-Eastern Italian Alpine district to detect their spatial and temporal (1973–2006) patterns. Moreover, a 1859 cadastral map was used to assess their patterns when agriculture was still widespread.

We tested the following hypotheses: (a) the herbaceous plant richness and density is associated with current and (b) historical landscape patterns of their habitat patches.

2. Study area

Our study area (46° 21' N, 10° 41' E) is located in Pejo which is a municipality located about 50 km northwest of Trento (Northern Italy). The Pejo municipality covers an area of 160 km² and belongs to the Subarctic Köppen-Geiger climate type with cool summers and dry winters. Average annual temperature in Pejo is 7 °C (altitude 1565 m) and average monthly temperature ranges from -1 °C in January to 15 °C in July. Precipitation is mainly concentrated in summer, the mean total being 856 mm. The geological substrate is siliceous metamorphic. This area is a Central-Eastern Alpine Italian region, completely included within or bordering the Stelvio National Park (Fig. 1). The landscape has evolved from the Roman culture (Fischer et al. 2008).

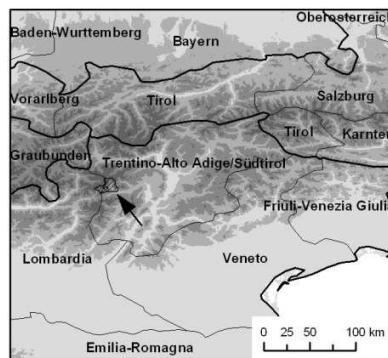


Figure 1 - Map of the eastern alpine regions with the location of the Pejo municipality

During the post-war period, the Province of Trento was affected by widespread socioeconomic changes which led to the abandonment of mountain agriculture and landscape transformation (Cernusca et al. 1998; Patella 1969; Pedrotti 1988, Tattoni et al. 2010). In the Pejo municipality the population decreased by 13% between 1951 and 1991 (Novello 2009) while forest cover increased by 26% (Ciolli et al. 2000, 2003). The twenty-first century has shown a slightly increasing demographic trend, but the employment rate in agriculture and livestock grazing is still falling. Agricultural change included the reduction in the number of farms and the intensification of agriculture in smaller areas, as well as fewer farmsteads (Provincia

Autonoma di Trento 2005). The current intermediate altitude belt consists of a matrix of larch and spruce forests and enclosed remnant grasslands. Some portions of these are still traditionally managed, rarely they have been completely abandoned. The formers are the so called *maggenghi* (Fig. 2).



Figure 2 – Particular of a *maggengo* of Masi Zampil in Pejo Valley (1664m a.s.l.(on the left) and picture of R. Albertini (1955), on the right, which reproduces a similar landscape to the study area (left side of Valfurva from Baite di Pradaccio di Sotto).

3. Methods

Patch delineation

Albertini (1955) produced a map with the precise location and a detailed description of the management of the *maggenghi* that at that time were in the study area. This author confirms that the management is the same in all the *maggenghi* and it is typical of this inherited anthropogeographic alpine landscape. Gathering information from land owners and rangers, from a digital 2006 orthophoto, from a vegetation map (Pedrotti et al. 1974) and a digital map of Natura 2000 habitats (Sitzia 2008) and from Pedrotti (1963) we were able to locate the approximate centroids of all the patches that corresponded to the *maggenghi* mapped by Albertini (1955) and were still managed. Within a buffer of 1 km around these centroids, we distinguished between areas of *maggenghi* and other soil uses from aerial orthophotos (1973–2006) and from the 1859 Asburgic historical cadastral map (Bednarr et al. 1859). We chose the interval of photos 1973–2006 to be sure that the *Trisetetum flavescens* association to which the community belongs had not changed since the historic vegetation map of Pedrotti et al. (1974) had drawn. The cadastral map was digitized by the Cadastral Service of Trento Province (Servizio Catasto 2006) while the vegetation map of Pedrotti et al. (1974) by the authors. A summary of the photographic and cartographic material is provided in Table 1.

Interpretation of photos and all the other spatial analysis were made using the GIS software ESRI® ArcMap™ 9.2 (ESRI 2006) at a fixed scale of 1:5000 to minimize mapping errors and with a 5 9 5 m cell as the basic unit. We chose this resolution to take into account the minimal possible mapping accuracy of about 1 mm which is 5 m on a map at scale 1:5000. The PatchMorph programming script (Girvetz and Greco 2007) was used to delineate patches from the resulting grid map using a neighborhood radius of 17.84 m and a threshold of 0.8 in the density filter mask and gap and spur thresholds of 10 and 0 m (2 and 0 cells) respectively. Finally, only polygons larger than 0.1 ha were retained as patches. These parameters were chosen because from the definition of secondary forest adopted by the Trento Province Forest Service (Sitzia 2009) follows that open fields enclosed by forests must be larger than 0.1 ha with a density

of trees lower than 20% and at least 10 m width (2 cells of 5 9 5 m) to be distinguished from forests in planning and conservation actions.

a)

Name of the flight	Date	Mean nominal scale	Focal length (mm)	Mean image resolution (m)
Rossi s.r.l.	11 Oct 1973	1:25000	153.12	1
Terraltaly 1994	13 Oct 1995	1:70000	152.82	1
Terraltaly™ 98/99	02 Oct 1999	1:40000	153.31	1
Digital Terraltaly™	01 Sep 2006	1:10000	62.5	0.50

b)

Description of the map	Reference	Date of field surveys	Scale	Type of classes
Asburgic Cadastral	Bednarr et al. (1859)	1859	1:2880	Land uses
Economic-pastoral map of the Ortles-Cevedale group	Albertini (1955)	1955	1:180000	Land uses and agricultural features (including maggengo meadows)
Vegetation of the Stelvio National Park	Pedrotti et al. (1973)	1961-1970	1:50000	Plant associations
Potential timberline of the Trento Province	Piussi (1992)	1987-1990	1:25000	Potential land uses
Natura 2000 habitats	Sitzia (2008)	2007-2008	1:10000	Natura 2000 habitats

Table 1 - Summary of digital aerial photos (a) and of maps (b) used to identifying the maggengo patches. The 1973-1995 photos are in black and white, while the 1999-2006 photos and the maps are in colour.

Plant survey

The patches were visited between June and September 2008 and a field protocol similar to that of Cousins et al. (2007) was adopted. To assemble data on patch species richness each site was walked through and all vascular plant species were recorded. The time spent at each site was adjusted to be proportional to the area of the site, approximately 30 min per ha. A specific survey of three rare species potentially present (*Lychnis flos-jovis* L.), *Festuca tenuifolia* and *Alopecurus geniculatus* L.) that would need more time to be found, was performed separately. Then, we surveyed species richness on ten plots of 1 m² placed along a transect of 15m with 0.5m between the plots. We surveyed a minimum of two transects and at least one per 1.5 ha, placed well apart from each other in representative portions of the patch, and at least 10m far from any field border to reduce the influence of edge effects.

Analysis

Avoiding redundant metrics, we calculated a set of key patch-based landscape metrics, interpreted as measures of patch compaction and edge irregularity (O'Neill et al. 1988; Riitters et al. 1995; Turner 1990;

Wang and Malanson 2007), and a connectivity index. Elongation index equalled l/w (Davis 1986; Forman 1995). Shape and perimeter-area fractal dimension indices were calculated as in McGarigal and Marks (1995) with the Patch Analyst 4 extension (Rempel 2008). We calculated the maximum nearest neighbor distances between the surveyed patches and all the other meadow-pasture patch centroids within a 1000 m radius. Within this distance we used the proportion of grasslands below the potential timberline, digitized from Piussi (1992), for every surveyed patch, as an index of connectivity (Kindlmann and Burel 2008). On each layer we measured the length of the axis (l) and the width (w) of the narrowest rectangle that enclosed each patch. We assigned to each patch its mean altitude, slope and its soil type according to the map of Aberegg et al. (2009).

We calculated two vascular plant diversity indices: patch interior species richness and species density. We considered interior species the shade-intolerant, i.e. those which were negatively affected in seedling germination and survival by changes in microclimate and light regimes (Geiger 1965; Laurance and Yensen 1991). From the total of 262 species, 202 shade-intolerant species were extracted following two subsequent steps: (1) 158 species having a Landolt (1977) indicator value for light ≥ 3 ; (2) a further 44 species having an Ellenberg (1992) indicator value for light > 6 . The following analyses were always referred to patch interior species. The degree of similarity between the patch species pools was assessed through the Sørensen's coefficient of community (Sørensen 1948) to permit a comparison with similar communities analyzed by Havlovà et al. (2004), while life spans were extracted from Kleyer et al. (2008). The species density (sensu Whittaker et al. 2001) was the average 10 m² plot species richness.

The relationships between size and 2006 patch interior species were summarized by the power, and by the exponential and logistic function, adopting the total interior species pool (202) as the upper asymptote (Tjørve 2003). The significance of the size, shape indices and connectivity trend along the 1973–2006 time sequence was tested with one-way ANOVA and, when significant, their influence on species diversity was also tested.

The topography factors frequently exercise great influence in grassland communities (Bennie et al. 2006; Klimek et al. 2007; Pykälä et al. 2005), together with soil heterogeneity (Reynolds et al. 1997). Thus, before performing the analysis with landscape metrics, we tested the correlation between species diversity and altitude and aspect even if, in this kind of communities, their effects should be reduced by the repeated management actions. For the same reason, we compared the species diversity means among the soil types as mapped by Aberegg et al. (2009).

Then we examined the correlation between the two dependent (current interior species richness and species density) and independent variables (landscape metrics). The independent variables included the landscape metrics that showed a significant trend from 1973 to 2006. As suggested by Waite (2000), only when the independent variables were not strongly correlated with each other and each was linearly correlated to dependent variables, their relative importance was tested using a multiple regression analysis. For correlation between linear variables we used the Pearson coefficient, while for circular-linear correlation the Mardia (1976) R^2 coefficient (Liddell and Ord 1978). To compare the means among the soil types we applied the Kruskal–Wallis H test.

Data deviating from a normal distribution was transformed by \log_{10} or was square root transformed, while proportions were arcsine transformed before analysis. All statistical analyses were performed with the Statistica 9.0 software (StatSoft, Inc. 2009), except for Sørensen's index that was calculated with

EstimateS 8.0.0 (Colwell 2006) and for the linear-circular analysis that was performed with Microsoft® Excel 2002. Species nomenclature is according to Pignatti (1982).

4. Results

Patch shape and pattern

The result of the aerial photos and cadastral map interpretation was a spatial database which included five temporal maggengo patch layers, i.e. 1859, 1973, 1995, 2000, 2006 (Fig. 3).

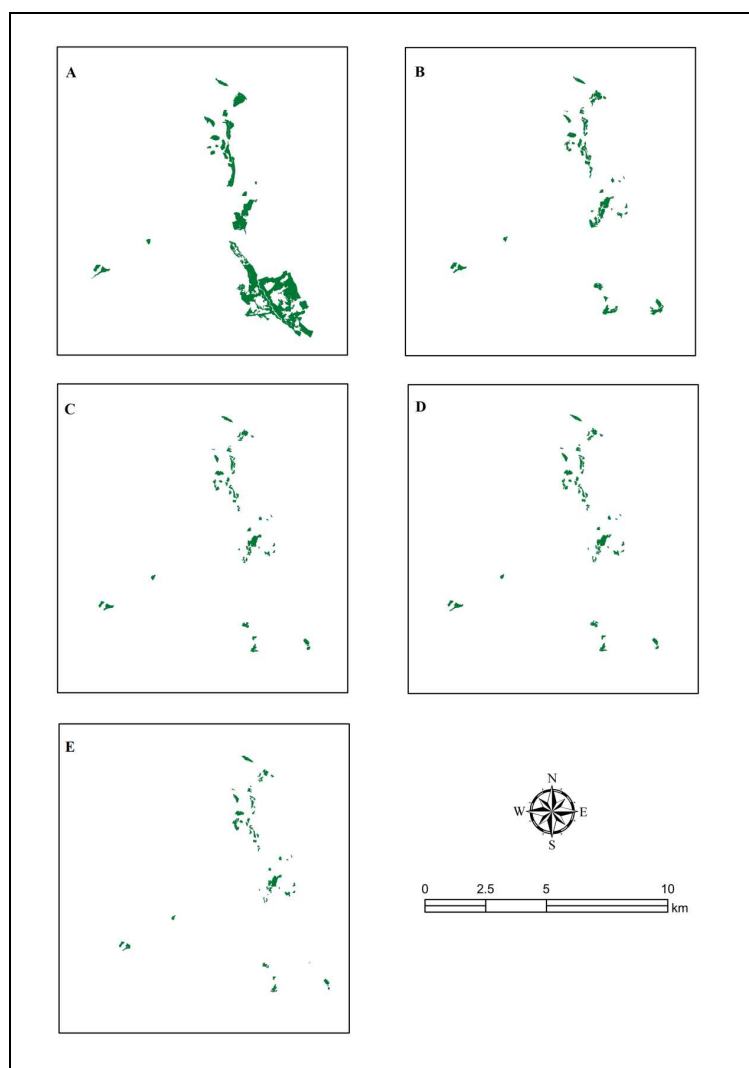
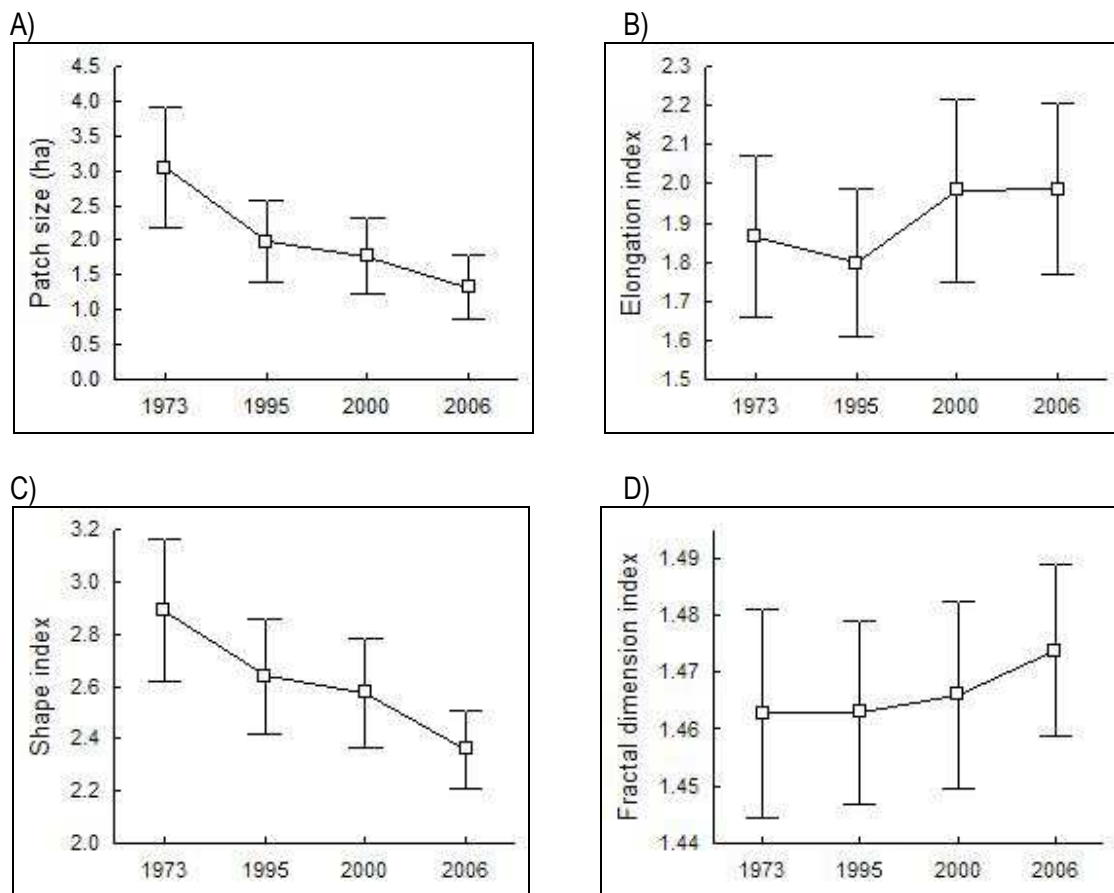


Figure 3 - Surveyed patch layers in 1859 (A), 1973 (B), 1995 (C), 2000 (D) and 2006 (E).

The total surface of the 59 current maggengo patches was 78.3 ha, and altitude ranged from 1250 to 2077 m (1565 ± 52 m, mean \pm 95% conf. lim.); aspect ranged from 43° N to 290° N (196° N \pm 31°). The current patch sizes ranged from 0.10 to 11.40 ha. The smallest and largest I were 45 and 685 m, while w

were 20 and 395 m, respectively. The elongation index varied between 1.09 (compact) and 5.00 (elongated). The shape index, varying between 1.47 and 3.99, denoted near circular patches. The fractal dimension index ranged between 1.36 (simple perimeter) and 1.65 (more complex perimeter). The maximum nearest neighbor distance was 527 m and was used as the radius for the calculation of connectivity (range 0.08–0.23). This 500-m buffer radius should exert the greatest influence on local plant populations (Tschamtkke et al. 2005).

From 1973 to 2006, the total patch size was reduced by 57% and fourteen 2006 patches resulted from the fragmentation of seven 1973 patches. Single patch size ($F_{(3,232)} = 5.5, p = 0.0012$), connectivity ($F_{(3,232)} = 17.0, p < 0.0001$) and shape index ($F_{(3,232)} = 4.3, p = 0.006$) revealed a significant trend, while elongation ($F_{(3,232)} = 0.8, p = 0.521$) and fractal dimension indices ($F_{(3,232)} = 0.4, p = 0.732$) did not show any significant trend (Fig. 4), therefore their relationships with species diversity were not analyzed. Among the landscape metrics, within the same year, only size and shape index were positively and always correlated ($r > 0.43, p < 0.001$).



E)

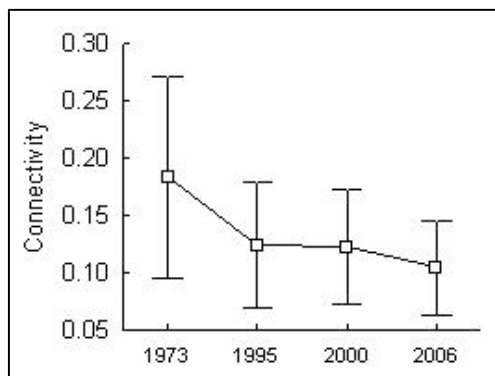


Figure 4 - Patch size (A), elongation (B), shape (C), fractal dimension (D) and connectivity (E) index during the period 1973-2006. Square denotes mean and bars 95% confidence interval.

From the 25 patches observed in 1859, twelve had split up into 39 smaller fragments and 13 had reduced in size without dissection or fragmentation in smaller fragments. Seven 2006 patches were not existent or were not portions of larger patches in 1859. Compared with today (Table 2), the 1859 patch size averaged 18.75 ha with a much wider range (0.7–186 ha), mean elongation and shape index decreased and had more variable values between patches, while fractal dimension differed slightly and connectivity averaged a higher value of 0.25 (± 0.03).

The current patch size and shape were not significantly correlated with those of 1859 (size: $r = -0.22$, $p = 0.115$; shape index: $r = 0.02$, $p = 0.883$), while the correspondent connectivities were strongly correlated ($r = 0.66$, $p < 0.001$).

Variable	Mean (conf. lim.)	
	current	1859
Size (ha)	1.32 (± 0.46)	18.75 (± 17.52)
Elongation	1.98 (± 0.22)	2.80 (± 0.95)
Shape	2.35 (± 0.15)	2.97 (± 0.99)
Fractal dimension	1.48 (± 0.02)	1.39 (± 0.02)
Connectivity	0.10 (± 0.01)	0.25 (± 0.03)

Table 2 Mean and 95% confidence limits for the current ($n = 59$) and 1859 ($n = 25$) size, shape, connectivity

Plant diversity

Forty-eight percent of the patch interior species were perennials; 13% were classified as perennials and annuals/poly-annuals; 13% as either annuals or biennials; life spans of 25% species were not available in the database used (Kleyer et al. 2008). Nine species, *Trifolium repens* L., *Potentilla erecta* L., *Achillea millefolium* L., *Trifolium pratense* L., *Plantago media* L., *Carum carvi* L., *Ranunculus acris* L., *Rumex acetosa* L. and *Nardus stricta* L., were observed in more than 80% of surveyed patches. Thirty-one species occurred in more than 50%, 42 between 20–49%, 32 between 10–19% and 96 in less than 10% patches.

The Sørensen's index has a mean of 0.48 ± 0.01 , with a minimum of 0.19 and a maximum of 0.87. Compared with data from similar plant communities (Havlovà et al. 2004), it confirmed the quite high similarity of meadow composition among the surveyed patches. Patch species richness ranged from 35 to 98 (58.3 ± 0.46 species), the interior one from 27 to 75 (44.5 ± 3.3 species), while species density ranged from 7.5 to 20.4 (14.2 ± 0.8 species/m²).

Patch interior species richness was significantly correlated neither with altitude ($r = -0.12$, $p = 0.37$) nor aspect ($R^2 = 0.04$, $p = 0.98$). Plant species density was not significantly related either with altitude ($r = -0.19$, $p = 0.16$) or aspect ($R^2 = 0.08$, $p = 0.96$). Neither patch interior species richness ($H = 3.66$, $p = 0.3$) nor patch species density ($H = 1.02$, $p = 0.76$) differed among the four soil types. We can then conclude that site variables do not exert any influence on plant diversity in our study area.

Relations of landscape measures with plant diversity

The fitted power function model provided the best fit to the species-area relationship ($F_{(2,42)} = 1313.11$, $p < 0.001$), and the 35% variation of the patch interior species was explained by the variation in patch size. The analysis suggests that the patch interior species richness S on patches was related to the size A (ha) of the patch and that the relationship conformed to $S = cA^z$, where $z = 0.09$, $c = 39.8$ (Fig. 5).

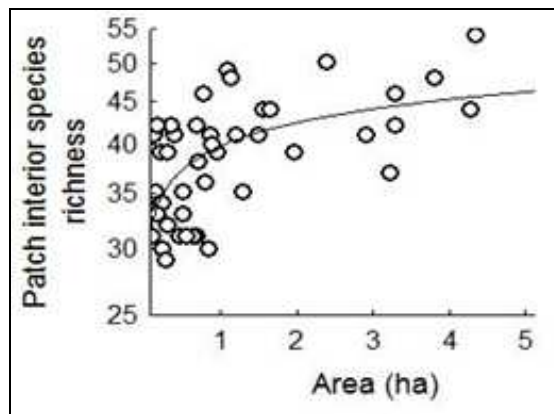


Fig. 5: Species-area relationships in maggengo patches (power function). The y-axis was log-transformed

Throughout the years spanning from 1973 to 2006, patch interior species richness was positively correlated with patch size and more strongly with the current, while with shape index it was positively correlated only at 2006. Connectivity showed positive correlation only with species density. The current patch interior species richness was not significantly correlated with any 1859 patch attributes, while species density was positively correlated with 1859 patch size, shape index and connectivity (Table 3).

a)

Patch metrics		Years				
		1859	1973	1995	2000	2006
Patch size	<i>r</i>	0.066	0.321	0.289	0.274	0.322
	<i>p</i>	0.640	0.023*	0.041*	0.049*	0.022*
Shape index	<i>r</i>	0.098	0.140	0.264	0.218	0.362
	<i>p</i>	0.488	0.332	0.063	0.128	0.010*
Connectivity	<i>r</i>	0.213	0.088	0.157	0.190	0.162
	<i>p</i>	0.130	0.543	0.275	0.188	0.260

b)

Patch metrics		Years				
		1859	1973	1995	2000	2006
Patch size	<i>r</i>	0.470	0.112	-0.144	0.008	-0.033
	<i>p</i>	0.001**	0.437	0.318	0.958	0.982
Shape index	<i>r</i>	0.390	-0.085	-0.021	-0.017	0.086
	<i>p</i>	0.006**	0.559	0.883	0.007**	0.544
Connectivity	<i>r</i>	0.410	0.455	0.439	0.455	0.544
	<i>p</i>	0.003**	0.001**	0.001**	0.001**	0.000***

Table 3 - Correlations of interior species richness (a) and species density (b) with patch size, shape index and connectivity, throughout the years spanning from 1973-2006 (* < 0.05, ** < 0.01, *** $p < 0.001$; d.f.₂₀₀₆ = 57, d.f.₁₉₇₃₋₂₀₀₀ = 56, d.f.₁₈₅₉ = 50).

Given the correlative statistics results, we performed a multiple regression model including current species density and only two independent variables: 1859 size and connectivity. This explained 49% of variation in the current species density and showed that the importance of size was relatively higher than connectivity (Table 4).

Variable	b	β	P
Intercept	2.78		< 0.001
1859 size	0.23	0.43	0.009
1859 connectivity	0.89	0.36	0.025

Table 4 - The multiple regression model for the effects of the 1859 size (log-transformed) and connectivity (arcsine transformed) ($n = 41$, $F_{(2,38)} = 20.81$, adjusted $R^2 = 0.49$, $P < 0.001$) on the current species density (squared transformed), (b: coefficients, β : adjusted coefficients).

5. Discussion

Patch shape and patterns

The study area was dominated, from 1973 to 2006, by the landscape process of maggenghi fragmentation, in terms both of reduction in the total area of habitat available and of breaking up of habitat that is left into remnants with different degrees of isolation (Saunders et al. 1991). Several studies have demonstrated that patch size and shape metrics depend on the pattern of fragmentation (Forman 1995). The fractal dimension trend over the period 1973–2006 was nearly flat, because the average irregularity of individual patches did not change within the range of forest expansion (or disturbance) rate, as demonstrated by Hargis et al. (1998) in simulated landscapes. Elongation index did not change in the same way because the contraction rate was almost even in width and length.

Among the major spatial processes that could have lead to the observed patch shape reduction, one that surely played a role along the time range analyzed was the spontaneous reforestation of the less accessible portions of the maggengo patches, i.e. the field lobes, which make boundaries curvilinear (Forman 1995).

Relations of landscape measures with patch interior species richness

Conforming to recent studies (Adriaens et al. 2006; Cousins and Eriksson 2008; Cousins et al. 2007) we might expect that the trends resulted from the analysis influenced plant species diversity, in particular species richness, or, as opposed to other studies (Cousins and Eriksson 2002; Grace and Guntenspergen 1999; Gustavsson et al. 2007; Helm et al. 2006; Lindborg and Eriksson 2004b; Mildén et al. 2007), that the historical landscape structure should, even in a changing landscape, influence present-day diversity. As reported in Klimek et al. (2007), this is particularly true especially where topographic variables did not have a strong influence on plant species diversity and management historical regimes didn't change in the time range analyzed (1973–2006), as in our study area.

Our results show that the 2006 size and shape index tend to explain the variation in patch interior species richness among the remaining maggengo fragments. The lack of correlation between the current and the 1859 size indicates that there was not a preferential abandonment rate depending on historical size, and, coupled with 2006 species-area relationship, this made it statistically impossible to find any influence of 1859 patch size on 2006 patch interior species richness.

The increase in patch interior species richness with increasing current patch complexity (shape index) was expected from other studies, which demonstrated the regularity in the effect of patch shape on patch interior species richness. This species-shape trend is known to be steepest for near circular patches (Heegaard et al. 2007), like the current ones. In contrast, the range of past shape values was not wide enough and their complexity too high to detect a significant correlation with patch interior species richness. The non-significant influence of grassland connectivity on patch interior species richness conforms to recent studies conducted in Alpine hay meadows (Marini et al. 2008a, b). The fact that patch interior species richness is influenced neither by the past nor by present connectivity is evidence that we had surveyed patterns that do not show an isolation effect.

This is, therefore, evidence of a plant extinction debt, or more precisely, a delayed plant extinction of long-living species (Krauss et al. 2004), as supported by the highest proportion of perennials which tend to form remnant population systems (Eriksson 1996).

Relations of landscape measures with species density

Neither size nor current shape attribute values were related to species density. Species density, in contrast, was related to connectivity, both current and past, and to historical size. Cousins and Eriksson (2008) suggest that if the past landscape connectivity and patch size were higher than present, high values of present species density are signs that the influence of historical landscape configuration still exerts an influence on plant diversity. In order to understand if our species density data is high, we performed a literature search. We found no data for the Alpine area, except for 5 m² plot density (Fischer et al. 2008); data surveyed on grasslands of California and Michigan (Harrison 1999; Gross et al. 2000) and a 9–11 range of species/m² reported by Stohlgren et al. (1999) in the Rocky Mountains, in a similar landscape and management context. Lacking better comparable study areas, the latter source allowed us to consider our species density value as being still high and made it clear that the historical signal from the 1859 size and connectivity is still existent.

Factors controlling species density includes the availability of nitrogen, other resources, various stresses, the species pool available to colonize the site (Gough et al. 2000), and the competitive intensity (biomass levels) (Shipley et al. 1991). Land use history (Grace 1999) and time lags in response (Melman et al. 1988) can also explain a portion of variability, as well as the time elapsed since the last disturbance event. Given that the management regimes and the site conditions were scarcely variable among the surveyed patches, these last three factors support the hypothesis that the 2006 pattern of species density has been shaped by a long continuity of management types, patch sizes and landscape context prior to the post-war general abandonment generated by socio-economical pressures. Species density must have reached a relative stability, even with a dynamic equilibrium, and, today, the numbers are still proportional to the historical landscape asset which has brought about, through long term dynamics, a fairly constant vegetation structure (Berlin et al. 2000; Gustavsson et al. 2007). This may be explained by the continuity of the impact of historical agricultural activities that have included the human driven movement of propagules in a more connected habitat (functional connectivity), which might have produced a more persistent species density (Cousins and Eriksson 2008; Hanski et al. 2004; Lindborg and Eriksson 2004b).

6. Conclusions

Our results confirm that where environmental site condition and management variables aren't determinants of plant species diversity, a significant amount of variation in the species data could be attributed to the pure effect of spatial variables (Borcard et al. 1992), which probably reflect historical processes (Svenning and Skov 2005). Moreover, changes in landscape pattern through long term dynamics could be one of the present plant species density determinants (Gustavsson et al. 2007). Also, Pykälä (2003) reported that species density was a more suitable indicator to evaluate spatial pattern changes effects on plant species diversity than species richness, which is generally more sensitive to environmental variables.

Some recent studies have concentrated on the management implications of landscape history legacy on semi-natural grasslands in Northern European rural landscapes. Our results suggest extending these kind of studies also to the fragmented mountain meadow-pasture communities within the predominantly forested landscapes of the European Alps.

Moreover, we suggest further research on the evolution of plant species communities through the critical analysis of the time series of quantitative botanical monitoring data, in study areas where significant spatial pattern changes are verified and over multiple scales, to incorporate emergent properties of the patch dynamics which could not be evident at local scale, as in our study (Wu and Loucks 1995). For its implications in conservation biology, this would be necessary to identify *taxa* threatened or lost due to the modifications in the landscape spatial patterns (see Cousins 2006; Gustavsson et al. 2007; Helm et al. 2006; Lindborg and Eriksson 2004b; Mildén et al. 2007).

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Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion

Trentanovi G., von der Lippe M., Sitzia T., Ziechmann U., Kowarik I., Cierjacks A. (2011) Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. *Manuscript*

1. Introduction

Urbanization is a globally increasing trend that profoundly changes ecosystems and biodiversity patterns (Alberti 2005; Kowarik 2011; McKinney 2008). A better understanding of the related consequences and underlying mechanisms is thus urgently needed for effective biodiversity conservation. In this context, biotic homogenization—the process of increasing taxonomic, genetic or functional similarities of formerly distinct regional biotas (McKinney & Lockwood 1999; Olden & Rooney 2006; Quian & Ricklefs 2006)—is a topic of increasing concern. In particular, the well-known richness of cities in nonnative species (Kowarik 1995; Pyšek 1998) has often been hypothesized to enhance biotic homogenization (McKinney 2006). As a consequence of increasing global exchange, the influx of the same suite of increasingly abundant nonnative species increases, while, at the same time, specialized native species in urban settings are extirpated (Kühn & Klotz 2006; McKinney 2006). Although cities may be richer in both native and nonnative species compared to rural surroundings (Kühn et al. 2004), the loss of native habitat specialists from urban habitats has been shown, which may reduce overall the distinctions between species assemblages and functional groups (Chocholoušková & Pyšek 2003; Duncan et al. 2011; Knapp et al. 2010). In addition to the regional spread of common exotic species, local dominance of exotic species may add to the homogenization effect of urbanization by competitive suppression of native species. Both drivers of taxonomic homogenization may be causally interrelated but this topic has rarely been addressed in homogenization studies.

While there is increasing evidence for urbanization effects on similarity patterns, homogenization studies have yielded divergent results thus far, differing among addressed taxa (e.g., plants, fishes or birds; Kühn & Klotz 2006; Luck & Smallbone 2011; Marchetti et al. 2006); regions (e.g., European and North American cities; La Sorte et al. 2008); and species groups included in similarity analyses (natives, nonnatives and subsets of the latter—with or without considering phylogenetic diversity (Knapp et al. 2008; Kühn & Klotz 2006; Ricotta et al. 2011)).

Previous studies ranged widely in scale, from continental (La Sorte et al. 2008) to local (Wania et al. 2006), but were all, to our knowledge, based on data sets from heterogeneous environmental settings such as species lists of total cities (Ricotta et al. 2011), more or less urbanized counties (Schwartz et al. 2006), or grid cells (Kühn & Klotz 2006). As even highly urbanized regions often encompass an array of semi-natural remnants as well as novel urban ecosystems (Kowarik 2011; Kühn et al. 2004), habitat heterogeneity is believed to strongly influence urban biodiversity patterns and may thus also overlay interrelated effects of species losses or gains on the similarity of species assemblages.

To disentangle the role of urbanization on the composition of species assemblages from effects of habitat heterogeneity at larger spatial scales, we aimed to explore homogenization due to urbanization and plant invasion at the community scale where species interact.

We chose woodland patches resulting from succession on urban grounds in Berlin as a model system and related the studied plots to characteristics of the surrounding urban matrix.

As exotic species may be both drivers and respondents of biotic homogenization (Kühn & Klotz 2006), we combined two approaches to include effects of plant invasions on urban similarity patterns. First, we sampled two types of urban woodlands, one dominated by a native tree species (*Betula pendula* R.) and the other by an exotic tree species (*Robinia pseudoacacia* L.). *Robinia pseudoacacia* is considered to be one of the top 100 woody plant invaders worldwide (Cronk & Fuller 1995). Second, we calculated floristic dissimilarity separately for total species, native species and nonnative species based on pairwise comparisons of plots of either woodland type. This combined approach enabled us to test for compositional differences in native and nonnative species assemblages in response to invasion of a dominant exotic pioneer and to assess if and how urbanity shapes these responses among species groups.

We hypothesized that:

(1) there are significant differences in alpha diversity of total, native and nonnative species pools in native *Betula pendula* woodlands in comparison to exotic *Robinia pseudoacacia* stands;

(2) exotic dominance leads to homogenization, i.e., reduced beta diversity, as indicated by a decrease in dissimilarity of total, native and nonnative species assemblages in comparison to *Betula pendula* woodlands;

(3) urbanity influences the dissimilarity of the total, native and nonnative species pools within both communities;

(4) there are combined effects of urban matrix components and *Robinia pseudoacacia* invasion on the dissimilarity among study plots that may affect the total, native and nonnative species pools differently.

By assessing these hypotheses, we were able to disentangle the relative contribution of plant invasions and the urban environment to homogenization in different species groups and exclude spatial heterogeneity of urban environments, which may obscure the underlying mechanisms.

2. Materials and methods

Study area

The study was carried out in Berlin (52° 24'N, 13°24'E), Germany, a city with 3.5 million inhabitants and an area of 892 km². In the natural landscape at the urban fringe, sandy, nutrient-poor soils prevail, whereas within the built-up-areas, soils predominantly reflect severe anthropogenic disturbance. Spontaneous urban woodlands, often dominated by either the native *Betula pendula* or the exotic *Robinia pseudoacacia*, have frequently developed on debris or gravel (e.g. Kowarik 1995). Overall, Berlin represents a complex urban matrix, comprising a variety of land uses, roughly 54% built-up areas, 21% woodlands, 12% green spaces, 6% water, 5% grasslands, and 2% arable fields (SenStadt 2008).

Study design

Ideally, biotic homogenization should be tracked over time by comparing historical and recent data. As such data are often unavailable, comparing invaded sites to nearby uninvaded sites is a common approach to provide a spatial analogue to temporal changes in communities before and after invasion (Sax 2002a). We thus relate current differences in diversity patterns of urban woods to homogenization of urban plant assemblages.

By using the area-wide habitat mapping of the federal state Berlin (SenStadt 2008), we randomly selected 34 pairs of woodland patches: one patch of the pair was dominated by the nonnative *Robinia pseudoacacia* and the other one by the native *Betula pendula*. Both woodland types result from spontaneous succession and are distributed over the total area of Berlin (Fig. 1). *Betula pendula* is a

frequent pioneer of temperate forests in Europe and one of the most successful species in spontaneous succession on manmade sites (Prach 1994). *Robinia pseudoacacia*, a forest pioneer native to North America (Boring & Swank 1984), is known to strongly change species composition in its nonnative range, mostly due to symbiotic nitrogen influxes (Dzwonko & Loster 1997; Von Holle et al. 2006).

We ascertained that the two patches within a given pair belonged to the same habitat type according to the map (i.e., pioneer forest and preforest) and were approximately of the same age to guarantee similar environmental conditions. Pairs that were assigned to the same habitat type were separated by a minimum distance of 1000 m to avoid spatial autocorrelation.

Within each woodland patch, we established a 10 × 10 m study plot, randomly located in the core area at a distance of >5 m from the border of the patch to counteract edge effects. The distances between both plots of a pair ranged from 20 to 500 m. We kept a minimum distance of 20 m between the edges of two matched plots to preclude neighboring effects, in particular nitrogen influx from *Robinia pseudoacacia* stands. At the same time, we did not exceed a distance of 500 m to assure similar environmental conditions for the pair.



Location of the plot pairs in Berlin. Enlarged square: example of a single pair of plots (black patch: *Robinia pseudoacacia* plot; grey patch: *Betula pendula* plot)

Vegetation data

Within each plot, all vascular plant species were recorded by the same persons to ensure equal sampling intensity. Species abundance was estimated by using the methodology of Braun-Blanquet (1964). All species were identified using standard literature for the German flora (Jäger & Werner 2005). We also visually estimated the canopy cover as this factor usually strongly affects regeneration processes in the ground layer. Species growing in the herbaceous and shrub layers were included in the statistical analyses, while tree species taller than 5 m in height were excluded as these had served as the criterion for patch selection. We differentiated between native and nonnative species according to the BioFlor database (Klotz et al. 2002). The group of nonnatives included archeophytes (pre-1492 introductions) and neophytes (post-1492 introductions).

Land use and habitat data

To explore the influence of the urban matrix on species assemblages, we identified the proportions of land use types in the surroundings of the study plots by using related information from the official habitat map of Berlin (SenStadt 2008). All values were calculated for the joint area of two 500-m buffers around the study plots of a pair. We determined the proportion of impervious surface, which included built-up area and road area. By subtracting road area, which is mapped separately, we obtained the built-up area, which was used to indicate different degrees of urbanity (hereafter referred to as urbanity). Following Knapp et al. (2009), we differentiated three classes of urbanity according to the proportion of built-up area: low (≤ 0.13), medium ($>0.13, \leq 0.34$) and high (>0.34).

Furthermore, we included the proportions of railway and road area as matrix variables. The Hansky index for woodland connectivity (Hansky 1994) between each plot and the ten nearest patches with the same woody vegetation was determined to assess the isolation of the studied patch. Both the proportions of railway and road areas as well as the Hansky index may play important roles in the homogenization of urban floras as they imply possible dispersal opportunities for organisms (Bierwagen 2007). As roads and the Hansky index for *Betula pendula* forests were not explanatory in the resulting models, data are not shown. Land cover calculation was performed using PatchAnalyst as an extension of ArcView GIS 9.2 software.

Statistical analyses

As a measure of alpha diversity, we calculated total species richness as well as richness of both native and nonnative species at the plot level. Moreover, we determined Shannon index and Simpson reciprocal index for each study plot; the latter is very suitable for the assessment of compositional differences (Lennon et al. 2001). We computed the reciprocal value of the Simpson index, as suggested by Kindt & Coe (2005) for biological communities with low diversity, and the Shannon evenness index. Beta diversity as a measure of species composition dissimilarity among communities is frequently evaluated using Jaccard's coefficient, which is based on presence/absence data (Olden & Rooney 2006). In this paper, we used Jaccard's distance, which shows the dissimilarity among species assemblages and is very adequate for detecting underlying ecological gradients (Faith et al. 1987). A plot-based beta diversity index was calculated by the average pair-wise Jaccard's distance of each study plot compared to all other plots of the same group (Vellend et al. 2007), i.e. to either all *Robinia pseudoacacia* or *Betula pendula* plots.

We tested for significant differences in species numbers of *Robinia pseudoacacia* and *Betula pendula* plots by using Mann-Whitney U-tests and performed Welch t-tests to check for differences in alpha diversity

indices; the latter test is frequently used for data sets with unequal sample variances (Ruxton 2006). Values of Shannon evenness and Simpson indices were log-transformed prior to analyses to normalize data. We furthermore tested the correlation between the richness of natives and nonnatives based on Spearman rank correlations for both forest types separately. Because the derived beta diversity metrics lacked independence, differences in beta diversity between *Robinia pseudoacacia* and *Betula pendula* plots were tested with a one-way permutation test, based on 9,999 Monte Carlo permutations. All alpha and beta diversity calculations were performed separately both for species groups (total species pool, natives, nonnatives) and for *Robinia pseudoacacia* and *Betula pendula* plots.

To test for influences of urbanity on beta diversity we assigned each pair of *Robinia pseudoacacia* and *Betula pendula* plots to one of the three urbanity classes and performed an approximative K-sample permutation test, based on 9,999 Monte Carlo permutations, followed by a Nemenyi-Damico-Wolfe-Dunn (NDWD) post-hoc test (for details see Hollander & Wolfe 1999).

To analyze the joint effects of *Robinia pseudoacacia* invasion, urban matrix variables and tree canopy cover on beta diversity, we performed boosted regression tree (BRT) analyses (Elith et al. 2008). We used BRT because of its high predictive power and its flexibility in handling both categorical and metric predictors. Mean Jaccard's distance was used as a dependent variable, while urbanity, proportion of railway areas, Hansky index for *Robinia pseudoacacia* stands, tree canopy cover, and *Robinia pseudoacacia* invasion (categorical, *Robinia pseudoacacia* vs. *Betula pendula* plots) were included as predictors in the models shown.

All statistical tests were conducted with R, version 2.7.2; diversity indices and dissimilarity measures were computed with the *vegan* community analysis package (Oksanen et al. 2009). NDWD test was calculated by using the package *multcomp*, while boosted regression trees were calculated with the package *gbm* and additional scripts provided by Elith et al. (2008).

3. Results

Alpha diversity

Species richness clearly differed between woodland types. Total species number of the shrub and herb layers was higher in *Betula pendula* than in *Robinia pseudoacacia* plots, and this also held true for the groups of native and nonnative species (Table 1). Correspondingly, average total species richness as well as average richness of native and nonnative species was significantly higher in woodlands dominated by the native tree species compared to exotic stands (Table 2). The richness in native species correlated significantly with the richness in nonnative species in both woodland types ($\rho = 0.444$, $p = 0.009$ in *Robinia pseudoacacia* plots; $\rho = 0.752$, $p < 0.001$ in *Betula pendula* plots).

Shannon and Simpson indices for alpha diversity also showed significantly higher values for total and native species in *Betula pendula* plots than in *Robinia pseudoacacia*, but no significant differences were detected for nonnative species (Table 2). Differences in evenness were less pronounced. The evenness of total and nonnative species was significantly higher in *Robinia pseudoacacia* plots than in *Betula pendula* plots.

	Black locust				Silver birch			
	Total number	%	Species number/plot		Total number	%	Species number/plot	
			Mean	SD			Mean	SD
Total	165	100	20.85	6.39	213	100	30.94	10.49
Indigenous	100	61	14.29	4.09	136	64	22.29	6.99
Exotic	65	39	6.56	3.52	77	36	8.59	4.18

Table 1: Overall species numbers found in 34 urban woodland plots (100 m²) in Berlin, dominated by the nonnative tree *Robinia pseudoacacia* and the native tree *Betula pendula*, respectively. Data for total species, native species and nonnative species

	Black locust	Silver birch	t	p
	Mean	Mean		
<i>Total species</i>				
Richness	20.85	30.94	4.72	<0.001
Shannon	2.02	2.34	2.99	0.004
Simpson	1.62	1.89	2.33	0.023
Evenness	0.71	0.66	-2.46	0.01
<i>Native species</i>				
Richness	14.29	22.29	5.67	<0.001
Shannon	1.72	2.15	4.17	<0.001
Simpson	1.38	1.79	3.59	<0.001
Evenness	0.72	0.68	-1.82	0.07
<i>Nonnative species</i>				
Richness	6.56	8.59	2.13	0.037
Shannon	1.16	1.3	1.13	0.26
Simpson	0.95	1.05	0.91	0.37
Evenness	0.78	0.71	-2.6	0.01

Table 2: Mean alpha diversity indices calculated for total species, native species and nonnative species of *Robinia pseudoacacia* plots (n = 34) and *Betula pendula* plots (n = 34), and results of Welch t-tests for differences between means

Beta diversity

For the total species pool we found no significant differences in beta diversity between *Robinia pseudoacacia* and *Betula pendula* plots (Table 3). This means that the dominance of an exotic tree species did not result in homogenization of associated species assemblages compared to stands of a dominant native tree species at similar urban sites. However, comparisons of native and nonnative species groups revealed divergent results (Table 3). For native species, beta diversity was slightly but significantly higher in *Robinia pseudoacacia* compared to *Betula pendula* plots, whereas for nonnative species, we found a lower beta diversity in the *Robinia pseudoacacia* plots.

	Mean β		z value	p
	Black locust	Silver birch		
Total species	0.82	0.82	-0.32	0.75
Native species	0.81	0.80	-2.07	0.037
Nonnative species	0.83	0.86	3.9	<0.001

Table 3: Comparison of Jaccard's distance (β diversity) between *Robinia pseudoacacia* and *Betula pendula* plots. Results from one-way permutation test

Effects of urbanity on beta diversity

Urbanity significantly influenced beta diversity of native species in both woodland types, and of total species in *Betula pendula* plots. However, beta diversity of nonnative species was not affected by urbanity in either of the woodland types (Table 4, Fig. 2). Beta diversity in the intermediate urbanity class mostly showed the lowest values, while highest dissimilarity was found in plots with low urbanity in their surroundings and the lowest proportion of built-up area. Corresponding to overall beta diversity, the total and native species pools of *Robinia pseudoacacia* stands showed higher Jaccard's distance values than those of *Betula pendula* stands in the plots that had been assigned to intermediate or high urbanity classes (Fig. 2).

	Black locust		Silver Birch	
	maxT	p	maxT	p
Total species	2.33	0.052	5.19	<0.001
Native species	2.67	0.017	5.87	<0.001
Nonnative species	0.47	0.883	2.13	0.082

Table 4: Significance level of the approximative K-sample permutation test for Jaccard's distance in three urbanity classes

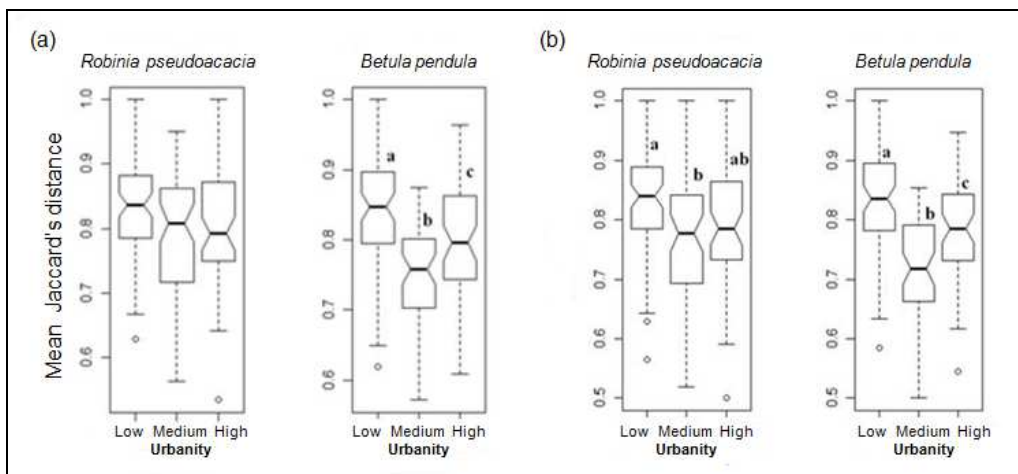


Figure 2 Influence of urbanity (low, medium, high) on the dissimilarity (mean Jaccard's distance) of species assemblages of urban woodland plots dominated by either the nonnative *Robinia pseudoacacia* or the native *Betula pendula* for (a) total species pool of *Robinia pseudoacacia* plots (NDWD test: P=0.054) and *Betula pendula* plots (NDWD test: P<0.001) and (b) for the native

species pool of *Robinia pseudoacacia* plots (NDWD test: $P < 0.005$) and *Betula pendula* plots (NDWD test: $P < 0.001$). Different lower case letters indicate significant differences. There were no significant differences for nonnative species (data not shown).

Joint effects of exotic dominance and urban matrix components on beta diversity

The joint effect of *Robinia pseudoacacia* invasion, urban matrix components and canopy cover on beta diversity of *Robinia pseudoacacia* and *Betula pendula* plots was analyzed by using BRTs. The analyses revealed that *Robinia pseudoacacia* invasion had nearly no relative effect on the mean beta diversity of the total species and native species pools (Fig. 3a, b). In contrast, *Robinia pseudoacacia* invasion was the most important predictor for beta diversity in nonnative species (Fig. 3c). Mean beta diversity in the total and native species pools was strongly influenced by the proportion of built-up area around the plots with the highest beta diversity at low proportions and the lowest beta diversity at intermediate levels of building density (Fig. 3a, b). Increasing proportion of railway areas generally enhanced beta diversity in all species groups but for total and native species there was an additional peak of beta diversity at extremely low proportions of railway area. Hanski connectivity between plots and tree dominated habitats increased beta diversity for all species as well as for native species whereas nonnative beta diversity peaked at intermediate connectivity and declined strongly at higher levels. Overall, these data provide evidence that the beta diversity of nonnatives strongly responds to *Robinia pseudoacacia* invasion, whereas the mean dissimilarity of the natives is more strongly related to urbanity.

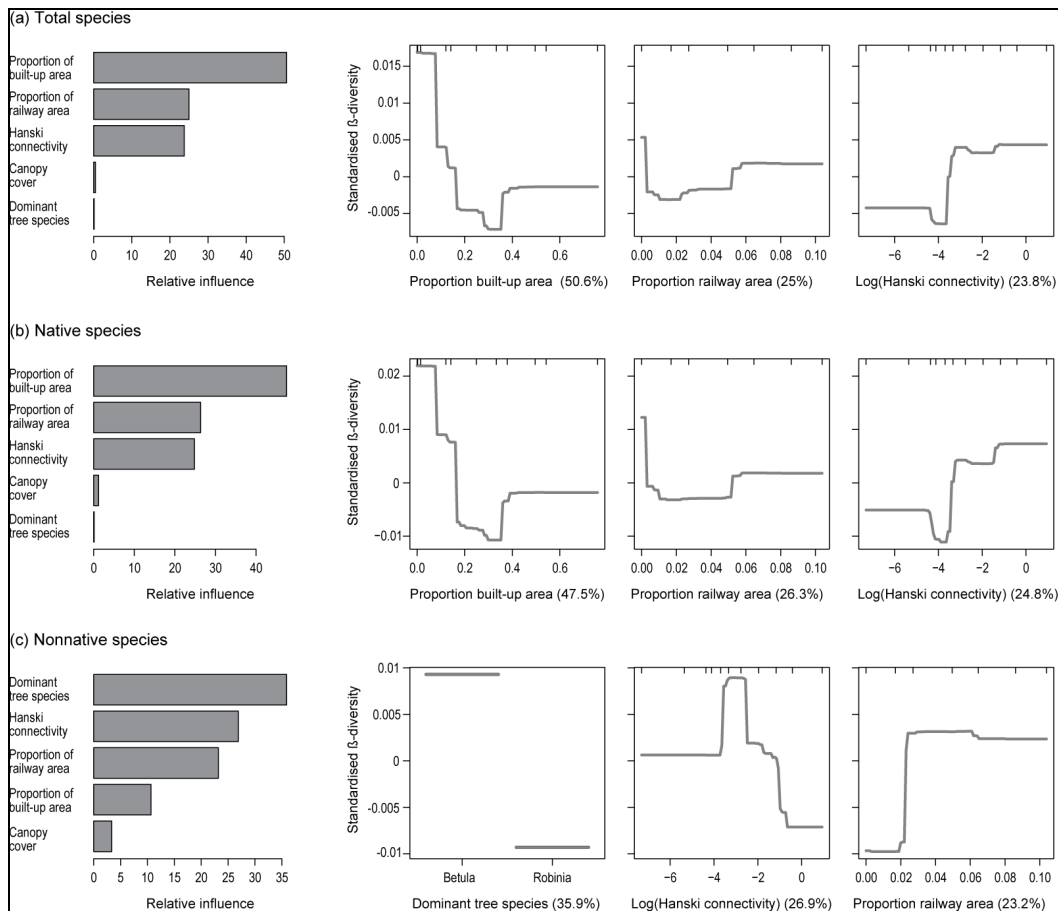


Figure 3: Relative variable importance plots and partial dependency plots for BRT analyses showing the size and direction of effects of matrix and site-related predictors on beta diversity for (a) the total species pool (cv correlation = 0.37 ; se = 0.13,

explained deviance: 0.27); (b) the native species (cv correlation = 0.41 ; se = 0.11, explained deviance: 0.36); (c) the nonnative species (cv correlation = 0.34 ; se = 0.13, explained deviance: 0.34).

4. Discussion

Effects of plant invasions on biodiversity patterns are strongly scale-dependent: while a range expansion of alien species will unavoidably lead to biotic homogenization at a global scale, nonnative species have been found to promote taxonomic differentiation at local to regional scales (Sax & Gaines 2003). Previous studies on urbanity effects on alpha and beta diversity of plant assemblages were based solely on data from heterogeneous land use or habitat types (e.g.; La Sorte et al. 2008; Schwartz et al. 2006). Given the large pool of nonnative species in cities (Kowarik 1995; Pyšek 1998), niche differentiation due to urban habitat heterogeneity increases the chance that, at intermediate spatial scales, many different nonnative species occur in many different habitats. Still, the generally lower abundance of nonnative compared to native species in urban areas (Chocholoušková & Pyšek 2003) likely amplifies taxonomic differentiation of urban areas. Correspondingly, a study related to the floristic inventory of 130 km² grids suggested taxonomic differentiation in nonnative species as opposed to a homogenization in native species assemblages of the most urbanized, compared to least urbanized, grid cells (Kühn & Klotz 2006).

Whether such similarity patterns also hold at the community scale has not yet been tested. In this study, we reduced habitat heterogeneity by using data from clearly defined vegetation types to disentangle effects of urbanization on the composition of plant assemblages from effects associated with habitat heterogeneity. Although differences presumably remain, e.g., in soils or habitat history of the sampled woodlands, our results reflect conditions that are clearly less heterogeneous compared to studies that comprise different land use types.

Alpha diversity of native and nonnative woodlands

While many studies have found hardly any differences in plant species richness among native and exotic woodlands (Michelsen et al. 1996; Sax 2002a), our study revealed a markedly higher species richness for native urban woodlands compared to stands dominated by *Robinia pseudoacacia*, both at local (average species richness per plot) and landscape scales (species richness of all plots; Table 1). Similarly, native woodlands also showed higher values for diversity indices for total and natives species than exotic woodlands (Table 2). As is the case for other nitrogen-fixing species, *Robinia pseudoacacia* is known to profoundly increase the nitrogen availability for associated species (Dzwonko & Loster 1997; Von Holle et al. 2006). This may be expected to enhance the species turnover compared to *Betula pendula* stands and promote a less diverse suite of competitive N-demanding species, ultimately resulting in lower species richness and diversity in the understory.

Interestingly, the native woodland plots had not only more native but also more nonnative species than the exotic woodland plots. Furthermore, the species numbers of the two groups were positively correlated. This adds evidence to the “rich get richer” hypothesis, which posits a positive correlation between native and exotic species richness (Stohlgren et al. 2003), although this has rarely been tested for forest types (but see Sax 2002b). Hence, the same factors that reduced native species numbers in *Robinia pseudoacacia* stands presumably also reduced nonnative species richness. Lower species numbers along with significantly higher evenness values of *Robinia pseudoacacia* plots suggest that a small number of N-demanding species—fostered by symbiotic N-influxes—prevail here and may outcompete other species with more specialized habitat requirements.

Yet our results clearly contrast with another study from rural settings that found a higher richness, due to a higher number of nonnatives, in *Robinia pseudoacacia* stands compared to native forests (Von Holle et al. 2006). While these results support the invasional meltdown hypothesis, which claims that secondary

invasions are promoted by positive interactions among invaders (Simberloff 2006; Von Holle et al. 2006), our contradictory results illustrate the strong context dependency of invasion impacts and can be explained by the fact that nitrogen availability is often higher in urban habitats than in the surroundings (Alberti 2005; Chocholoušková & Pyšek 2003), and certainly also compared to the nutrient-poor sandy soils that prevailed in the study area of Von Holle et al. (2006).

Beta diversity of exotic compared to native woodlands

The marked decline of alpha diversity in the exotic stands corresponds to a general pattern showing a reduction in diversity of resident species assemblages owing to invading species (Vilà et al. 2011). In contrast to our expectations, the strong decrease in total species richness and alpha diversity measures due to *Robinia pseudoacacia* dominance at the plot level did not go along with a general decline in beta diversity at the community scale. We found no homogenizing effect and consequently similar beta diversity of *Robinia pseudoacacia* stands for the total species pool and, for native species, even an increase in beta diversity, compared to native *Betula pendula* woodlands. As the decline in species richness was most pronounced in native species, this opposing result for beta diversity can only be explained by a random suppression of native species in the exotic woodland plots. As Jaccard's distance between study plots is generally independent of species richness, increased values of this index along with a decline in alpha diversity indicate that previously shared native species become locally extinct. On the other hand, nonnative species' beta diversity was significantly lower in *Robinia pseudoacacia* plots, which points to a homogenizing effect of the dominant invader on the associated nonnative species assemblages. Hence, in contrast to its effect on native species, *Robinia pseudoacacia* seems to facilitate a common nonnative species pool as already suggested by Von Holle et al. (2006).

Our data show that the loss of native species in exotic woodland patches does not translate to biotic homogenization in associated native species assemblages but in communities of nonnative species. While nonnative species were found to enhance differentiation of urban floras at larger spatial scales (Kühn & Klotz 2006), our study clearly demonstrates that such findings on urban similarity patterns cannot be generalized for the community scale.

Differences in beta diversity among urbanity classes

Previous studies analyzed effects of urbanization on beta diversity of species assemblages mostly by characterizing the sampled areas with parameters that are frequently related to urbanization such as percentage of impervious surface. In this case, again, differences in the ecological characteristics of the sampled areas, which are not covered by urbanization parameters (e.g., differences in site history between natural habitat relicts and novel urban ecosystems), may overlay biodiversity responses to urbanization. We reduced this heterogeneity by relying on similarity patterns in plant assemblages at the community scale.

In accordance with results from heterogeneous urban environments at larger spatial scales (Kühn & Klotz 2006), the highest beta diversity mostly corresponded to the lowest urbanity class. This held for native species in both exotic and native woodlands and also for total species in native woods (Fig. 1). Our results thus clearly add evidence to the idea that urbanization promotes homogenization of native plant species assemblages.

An unexpected result was the absence of effects of different levels of urbanization on similarity patterns in nonnative species. We found homogenization effects in nonnative species assemblages of the *Robinia pseudoacacia* stands (see above), but these appear to occur independently from the urbanization level in the plot surroundings.

Surprisingly, we observed the lowest beta diversity for total and native species in the intermediate urbanity class. Most studies on urban–rural gradients have found that intermediate levels of urban development are often related to highest species richness (McKinney 2008), and at larger spatial scales, the similarity in native species in urban regions decreased directionally with decreasing levels of urbanization (Kühn & Klotz 2006). This pattern obviously did not translate to the community scale in our study. Although efficient dispersal vectors such as traffic move seeds of nonnatives and natives in urban settings (von der Lippe & Kowarik 2008) and many native plant species are usually present in areas subjected to intermediate levels of urbanization (McKinney 2008), this variety did not contribute to the differentiation of species assemblages in the studied wood patches. As these were all successional woods on urban grounds, we can fairly exclude remnants of native forest species. Instead our study suggests the functioning of an environmental filter (presumably shade) that limits the colonization of urban woods by species not adapted to this condition—even in likely species-rich surroundings. This also holds for nonnative species as suggested by another key finding of our study: urbanization did not affect similarity patterns in nonnative species in both studied woodland types.

Joint impacts of urban matrix components and exotic dominance on beta diversity

The BRT analysis shed light on the relative importance of different urban matrix parameters and exotic dominance in the tree layer on the taxonomic similarity among the addressed species groups (Fig. 2). The main result was that different parameters shape homogenization in native (and total) species groups and nonnative species groups indicating functional differences between them. This would correspond to urbanization-induced changes in functional trait representation in native and nonnative species assemblages that have been found at larger spatial scales (Knapp et al. 2008; 2010; Ricotta et al. 2011).

In accordance with findings on the impact of urbanity on homogenization, the beta diversity of both the total and the native species pools clearly responded to the proportion of built-up area with the lowest beta diversity in intermediate urbanity levels. Also the dispersal-related parameters (proportion of railway, patch connectivity) exhibited a pronounced impact, whereas stand-related parameters were not important for beta diversity of native species. Intermediate proportions of railway areas around the patches decreased beta diversity, while higher patch connectivity promoted beta diversity in native species. These results suggest that biotic homogenization in the native species pool of our model systems was increased by components of the urban matrix including those that promote patch connectivity and species exchange. Still, the high contribution of the proportion of built-up area to homogenization in the native species group may indicate dispersal limitation, which led to a reduced species pool in plots that were located in highly urbanized surroundings.

Exotic dominance did not foster homogenization in native species assemblages but was the most important parameter for homogenization of the nonnative species pool. In contrast to native species, nonnative beta diversity peaked at intermediate patch connectivity while high connectivity strongly homogenized the species assemblages. This suggests the functioning of an exchange of common nonnative species between urban woodland patches that appears to foster taxonomic homogenization only in highly connected patches. Results from larger spatial scales similarly illustrated a functional homogenization in species traits in urban species assemblages and an increased representation of species with traits related to a higher potential of long-distance dispersal (Knapp et al. 2008, 2010). Different from patch connectivity, the proportion of railway area around the patches promoted nonnative beta diversity. This indicates a more diverse nonnative species pool in railway habitats compared to neighboring woodland patches with a potential to colonize and differentiate the urban woodland patches.

Overall, our study revealed significant effects of urbanization, exotic dominance and habitat connectivity on diversity values at the community scale, yet with divergent responses in total, native and nonnative

species assemblages. Our results add evidence to the general insight that urbanization can enhance biotic homogenization, but we also demonstrated effects of taxonomic differentiation, depending on the addressed species group and woodland type. Downscaling similarity analyses at larger spatial scales to the community scale can thus lead to different insights in the functioning—and outcome—of mechanisms driving biotic homogenization.

Maintaining diverse species assemblages in steadily growing urban areas is an increasing challenge for nature conservation. In this regard, revealing homogenization trends at the community scale is highly relevant as species mostly interact at this scale. Our results on successional urban woodlands clearly show that the spatial context of urban habitat patches is important in homogenization processes. Therefore, urban planning should take the homogenization aspect into account and aim at spatial structures that reduce the risk of biotic homogenization. As biotic homogenization is a temporal process, it is a challenge for further studies to test for changes in diversity patterns during ongoing succession and for portability of these results to other semi-natural vs. specifically urban ecosystem types within urban regions to enhance the understanding of mechanisms that drive urban biodiversity.

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PAPER IV

Cultural system as determinant of hedgerow structure and woody species richness

Sitzia T., Trentanovi G., Marini L., Cattaneo D., Semenzato P. (2011) Cultural system as determinant of hedgerow structure and woody species richness. *Landscape and Urban Planning*, *under review*

1. Introduction

Semi-natural habitats often provide the only element of structural and biological diversity in landscapes that have lost most of their naturalness to agriculture (Burel 1996). Many studies found that hedgerows support a broad range of different wild animal (e.g. Mauremooto et al. 1995, Paoletti 1995, Tattersall et al. 2002, Whittingham et al. 2005) and plant species in intensive agricultural and suburban landscapes (e.g. Forman and Baudry 1984, Manzini 1989, McCollin et al. 2000, French and Cummins 2001, de Blois et al. 2002, Sitzia 2007), where they play an important role in shaping the patterns of connected landscape elements, both physically and functionally (Antrop 2000, Treu et al. 2000, Botequilha Leitão and Ahern 2002, Padoa-Schioppa et al. 2006, Sánchez et al. 2010).

Hedgerows with a large diversity of shrub and tree species are expected to support a great abundance and diversity of associated organisms such as birds (Macdonald and Johnson 1995, Hinsley and Bellamy 2000, Padoa-Schioppa and Chincarini 2007) or invertebrates (Maudsley 2000). The richness of the woody species is influenced by several environmental factors such as age, size, management, and vertical structure of the hedgerow (Hooper 1970, Willmot 1980, Sutton 1992, Herlin and Fry 2000, Boutin et al. 2002, Deckers et al. 2004a, Deckers et al. 2004b, Campagne et al. 2006). Trees and shrubs are usually maintained or planted by farmers through routinely or regulatory practices (Sutton 1992, Burel and Baudry 1995). Regeneration and tending methods and/or the rotation period produce different growth forms: shrubs, pollards, coppices and high trees whose arrangement should be viewed as a cultural system, affecting the hedgerow structure. The latter is often in direct relation to the habitat value (Hinsley and Bellamy 2000).

The main aims of this study were (i) to investigate how four different cultural systems (low-single storied, high single-storied, two-storied; and multi-storied) differ in hedgerow structure and (ii) to identify the main management-related determinants of native woody species richness. Specifically, a large dataset was used, including data from more than 500 hedgerows, pertaining to intensive agricultural landscapes, to investigate how management of different cultural systems determines various hedgerow structural features and the richness of native woody species.

2. Methods

Study area

The Veneto plain is a sub-region of the Padana plain, located in the north-eastern part of Italy covering an area of about 10,372 km² (Fig. 1). Mean annual precipitation varies between 700 and 1100 mm and the mean annual temperature is from 13 to 13.5°. According to the bioclimatic criteria of Rivas-Martines (1995), the Veneto plain is located in a transitional area between Temperate and Mediterranean climatic zones. The Veneto plain has been subjected to substantial transformations that have modified the structure of the landscape, from the Roman centuriation in the 1st century BC, to the industrial settlements of the 1970s (Tempesta 2010). Nowadays 49-85% of the provincial areas are agricultural and the dominant culture is maize, soybean, others cereals and wine grapes (Vonghia 2006).

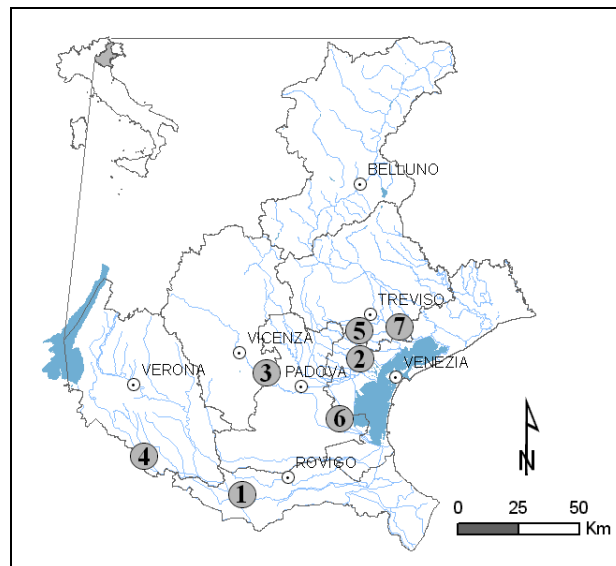


Figure 1 - Italy, Veneto region and location of the surveyed sites (1: Canda, 2: Frassinelli, 3: Montegalda, 4: Nogara, 5: Peseggia, 6: Piove di Sacco, 7: Roncade)

Sampling

We surveyed seven sites scattered in the Veneto plain (Table 1 and Fig. 1) where hedgerows had been established or modified in different periods, and where spontaneous regeneration of plant species was possible (Zanaboni and Lorenzoni 1989).

Sites	Provinces	Municipalities	Surveyed areas (ha)	No of hedgerow surveyed	Hedgerow densities (km 100ha ⁻¹)
Nogara	Verona	Nogara, Gazzo Veronese, Sorgà	625	59	2.7
Rovigo	Rovigo	Canda, CastelGuglielmo	4572	68	0.85
Piove	Padova	Piove di Sacco, Arzegrande, Brugine, Pontelongo	420	107	6.97
Frassinelli	Venezia	Martellago, Spinea, Venezia	158	47	8.67
Peseggia	Treviso Venezia	Zero Branco, Scorzè	175	59	8.14
Roncade	Treviso	Roncade	645	106	3.79
Montegalda	Vicenza	Grisignano di Zocco, Montegalda	627	92	3.92

Table 1 - Surveyed sites

Generically a hedgerow was defined as a row of woody plants, including hedge and herbaceous species, that separates adjacent fields (Pollard et al. 1974, Forman and Baudry 1984) and is more or less managed (Baudry et al. 2000). In this study we adopted a definition of hedgerow based on different sources (Bidese and Peruffo 1993, Bickmore 2002), which considers some spatial attributes such as length (minimum length of 20 m) and threshold for width at widest point of canopy (maximum of 30 m) and gap percentage (maximum of 35 %) (Table 2). A gap exceeding 20 m implies that the sections on either side of gap are separate hedgerows. Ornamental edges and roadside planted strips were excluded.

Measure	Threshold	Reference
% gap	< 35 %	Bickmore (2002)
Gap length	< 20 m	Bickmore (2002)
Hedgerow length	> 20 m	Bickmore (2002)
Hedgerow width	< 30 m	Bidese and Peruffo (1993)

Table 2 - Thresholds used to define a hedgerow

We defined four hedgerow cultural systems which were classified according to the arrangement of plant growth forms as follows (Fig. 2): multi-storied (shrubs, pollarded trees and coppice), high single-storied (pollarded trees and high trees or only pollarded trees or only high trees), low single-storied (shrubs and coppice or only coppice or only shrubs) and two-storied (pollarded trees and shrubs or pollarded trees and

coppice or high trees and coppice). We randomly selected the hedgerows within the four cultural systems within each site accordingly to their frequency, ranging from a minimum of 47 samples to a maximum of 107 (Table 1). A total of 538 hedgerows were surveyed (Table 1). All the sites are nearly flat, being 63 m a.s.l. the highest elevation in the Montegalda site.

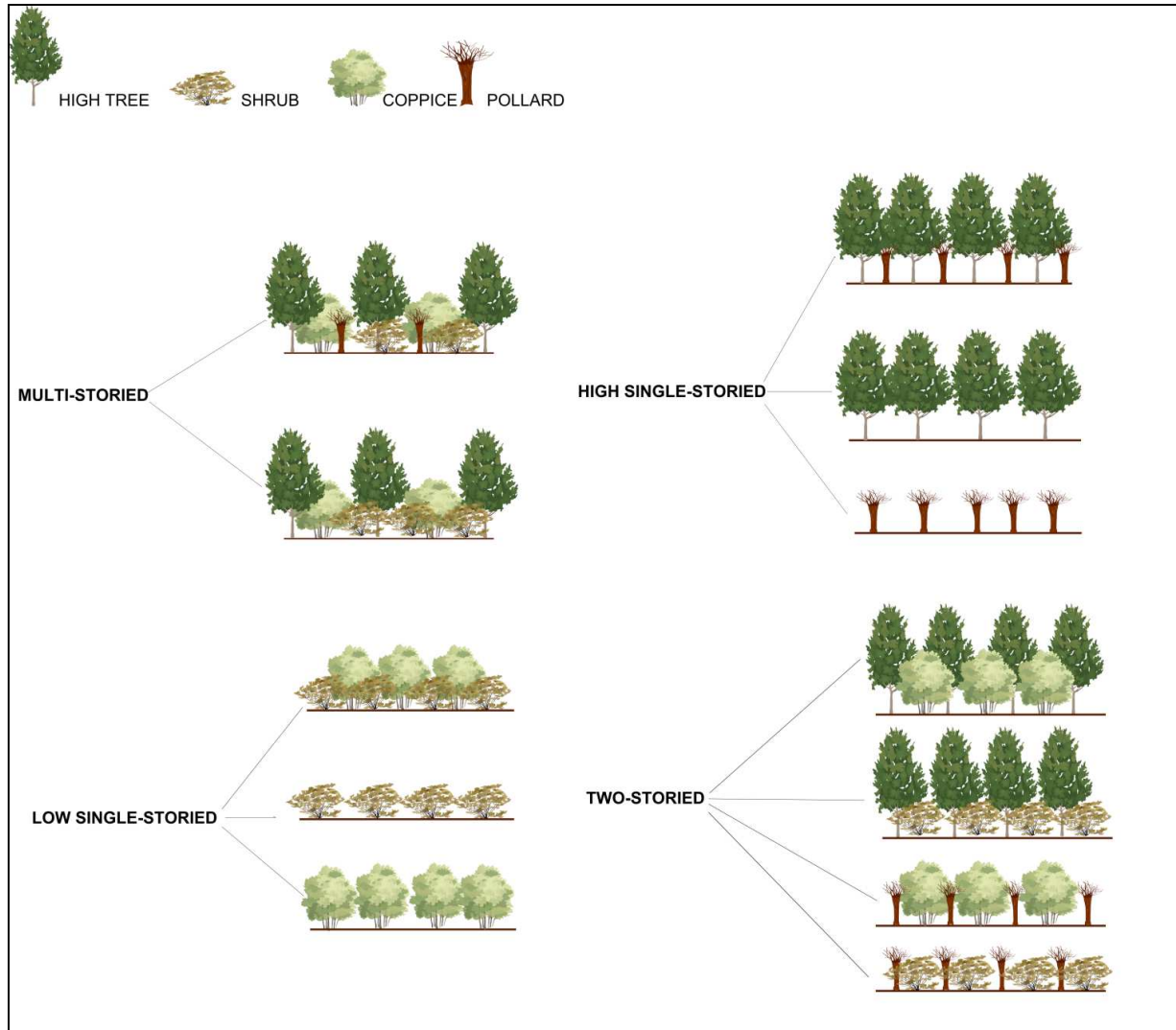


Figure 2 - Hedgerow's cultural systems: multi-storied; high single-storied; low single-storied; two-storied.

Data on woody species richness

The presence and absence of woody species was determined by surveying each hedgerow and identifying every species classified as tree or shrub by Pignatti (1982).

Structural characteristics of the hedgerow

Along with the four explanatory variables we further gathered the following environmental variables. The hedgerows were divided into units of equal length based on their total length (one plot for hedgerows with a length < 100 m; two plots for hedgerows with a length between 101 and 300 m; three plots for hedgerows with a length between 301 and 600 m; four plots for hedgerows with a length > 600 m). Within 10-m transverse plots of hedgerows, centered on the resulting units, four variables were measured and averaged for each hedgerow: number of trees, diameter at breast height, height, and the width at widest point of canopy (called simply width) of all living trees (DBH > 5 cm). We calculated the area (length of the entire hedgerow \times width) and the basal area (mean values per 1 ha of hedgerow) for each hedgerow surveyed. Finally, we calculated also two indices of height and diameter diversity, i.e. the Shannon index (Shannon 1948) and the Gini coefficient (Latham et al. 1998). Both indices have been previously used in forest management and planning, and the Gini coefficient is the only index whose sensitivity to sample size is very low (Lexerod and Eid 2006).

All data were integrated in a GIS environment with ArcView GIS 9.2 (ESRI 2006), and hedgerow density (m km⁻²) was calculated. The density is related to the different agricultural landscape assets and histories, from the ancient agricultural landscape of Roman centuriation to the intensive agricultural lands reclaimed in the Early and Late Medieval Ages or in more recent times (Tempesta 1989, Meeus et al. 1990, Regione Veneto 2007).

Data analysis

Differences between the structural features were tested through one-way ANOVA for each hedgerow cultural system. Data deviating from normal distribution were log or square root transformed before the analysis. We applied general linear mixed model to test the effect of area, cultural system and basal area on the number of woody species, classified as native by Pignatti (1982), identified in the hedgerows. The model included area, cultural systems and basal area and their interactions as fixed effects, and site as random effect to account for spatial nestedness in the sampling. The interaction between area and cultural system was tested to see whether the different cultural systems change the slope of the species area curve (SAR). The interaction between cultural system and basal area were tested to verify whether the effect of increasing basal area on native woody species richness was different within the different cultural systems.

As suggested by Pinheiro & Bates (2000), a sequential F-test was used to investigate the main effects and interactions in all models using the `lme(nlme)` function (Pinheiro et al. 2010) in R with the restricted maximum likelihood (REML) estimation method. All statistical analysis were performed in R (R Development Core Team 2011).

3. Results

Eleven woody species had a frequency >40% in the total number of hedgerows: *Salix alba* L., *Cornus sanguinea* L., *Platanus hybrida* Brot., *Sambucus nigra* L., *Rubus ulmifolius* Schott, *Robinia pseudoacacia* L., *Acer campestre* L., *Ulmus minor* Miller.

Hedgerow structure differed significantly between the four cultural systems (Table 3). Multi-storied hedgerows had the highest values of size as well as both Shannon and Gini diversity indices. Otherwise the highest values of tree basal area/ha and of the number of trees/ha referred respectively to the high single-storied and low-single storied cultural system.

	Low single-storied (n=123)		High single-storied (n=90)		Two-storied (n=130)		Multi-storied (n=195)		F	P
	mean	SD	mean	SD	mean	SD	mean	SD		
Lenght (m)	152.7	109.7	149.7	120.84	147.1	121.6	214.0	158.7	12.8	*
Width (m)	4.8	1.8	5.3	1.7	5.5	1.6	6.5	2.3	21.4	*
Area (m²)	754.9	697.0	795.4	687.0	821.8	737.6	1358.1	1054.0	24.2	*
Basal area (m² ha⁻¹)	22.7	31.2	55.5	89.7	38.8	49.5	35.5	31.9	12.2	*
No trees ha⁻¹	4268	4439	1814	1638	2464	3039	2278	1861	19.3	*
SHD	1.37	0.60	1.66	0.58	1.51	0.63	1.97	0.56	31.1	*
SHH	0.99	0.55	1.03	0.55	1.19	0.58	1.49	0.50	28.3	*
GINID	0.09	0.07	0.08	0.08	0.12	0.08	0.13	0.05	17.6	*
GINIH	0.15	0.1	0.18	0.10	0.21	0.13	0.28	0.12	35.6	*

Figure 3 - Effect of the four cultural systems on native woody species richness. The dot indicates the mean while the solid line indicates the median.

	df	F	P
Log(Area)	1, 526	284.74	<0.001
Cultural systems	3, 526	38.358	<0.001
Log(basal area)	1, 526	4.518	0.034
Cultural systems x Log(Area)	-	-	-
Cultural systems x Basal area	-	-	-

Figure 4 - Effect of hedgerow area on native woody species richness. Each plot represents one sampling site (see Table 1).

Results of the mixed models (Table 4) showed a high significant effect of hedgerow area ($P < 0.001$) and cultural system ($P < 0.001$) on native woody species richness, as well as a marginal effect of basal area ($P = 0.034$). Multi-storied support the highest number of species followed by two-storied hedgerows. High single-storied cultural system contains the lowest number of species (Fig. 3). Interaction between area and cultural system, as well as the interaction between basal area and cultural system, were not statistically significant. The slope of the relationship between hedgerow area and native species richness was positive and did not differ between the four cultural systems (Fig. 4). On the contrary, basal area showed a marginal negative effect on native woody species richness after accounting for the effects of area and cultural system.

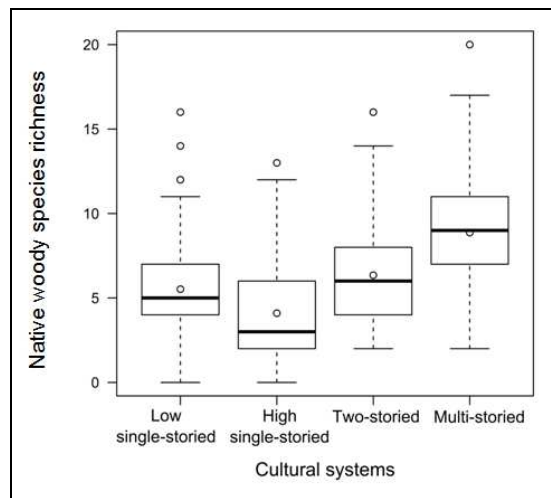


Figure 3 - Effect of the four cultural systems on native woody species richness. The dot indicates the mean while the solid line indicates the median.

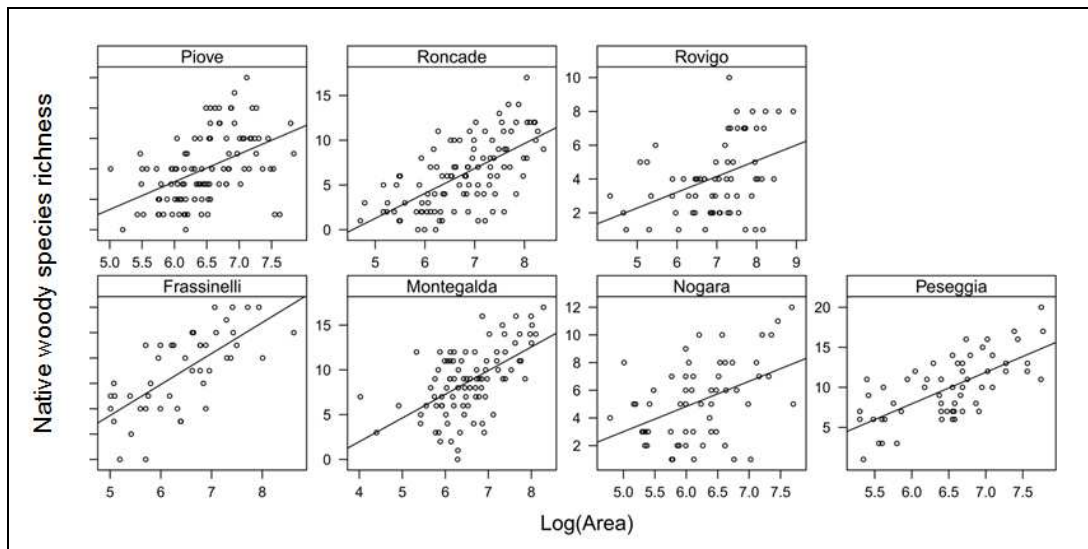


Figure 4 - Effect of hedgerow area on native woody species richness. Each plot represents one sampling site (see Table 1).

4. Discussion

Each cultural system considered in our study showed a relationship with the various hedgerow structural characteristics. In addition, hedgerow cultural system, area and basal area exerted great influence on both structural features and native woody species richness.

The presence of several or diverse growth form guarantees per se a higher vertical stratification as confirmed by the differences in the diversity indices, basal area and tree density among the four cultural systems. Indeed management practices are typically characterized by a frequency and intensity of cyclic cuttings along the hedgerow linked to customs more than to rules, resulting both in different vertical tree layers successions and structural variables values. The highest values of the two indices of diameter diversity are associated with the multi-storied system as reported in many studies referring to forest stands where the presence of a multi-layered canopy relates to a large variety of stem diameters and heights, and a complex horizontal arrangement of stems (McElhinny et al. 2005). Similarly in our study the highest values of basal area were found in the high-single storied cultural system.

As well documented for forests (Pretzsch 1997, Brokaw and Lent 1999), ecosystems containing stands with a variety of structural components are considered likely to have a variety of resources and species that utilize these resources. Thus, the positive correlation between elements of biodiversity and measures of complexity within an ecosystem can be extended to hedgerow systems, where the more complex vertical spatial arrangement of tree canopy resulting from the multi-storied hedgerow cultural system supports a higher variety of woody species. These results are consistent with those of Franklin et al. (2002), who found that species composition and abundance can be indicators of canopy layering. Both high single-storied and low single-storied hedgerows contain less woody species, as reported in similar studies on forest stands (e.g. Nordlind and Ostlund 2003). Microclimate conditions, the intensity and quality of light, resources availability and others ecological variables can explain this relationship between tree canopy structure and species richness (e.g. Parker and Brown 2000). These findings extend previous evidences of the relations between woody species richness with a variety of local hedgerow attributes (Willmot 1980, Sutton 1992, Herlin and Fry 2000, Deckers et al. 2004a, Campagne et al. 2006) also to the spatial arrangement of tree and shrub growth forms). This study indicates that the identification of cultural systems, obtained through a visual survey, may allow estimating native woody species richness across a wide range of hedgerow network densities and landscape types, favoring the interaction between decision makers, researchers and users of the landscape (Vos and Meeke 1999).

Both the effect of hedgerow area and tree basal area on woody species richness was not affected by hedgerow cultural system. Species accumulation with increasing area is a well know phenomenon also for hedgerows (e.g. Deckers et al. 2004a). Tree basal area is a correlate of stand volume and biomass that we can interpret as saturation level (sensu Shorrocks and Sevenster 1995). Due to the narrowness and homogeneity of hedgerow area, we can hypothesize that high values of basal area tend to saturate the niche space faster than in a more complex habitat, i.e. a woodland, where we can notice sometimes a opposite trend (Risser and Rice 1971, Liang et al. 2007).

Management implications

Management implications for woody species richness conservation derive from the above mentioned considerations. In regard to cultural systems, the conversion of high single-storied and low single-storied hedge to multi-storied hedgerow should be promoted. These silvicultural practices are well known in forest management (Buongiorno et al. 1995, Hanewinkel 1998), but they are seldom applied to hedgerow systems. As Bannister and Watt (1995) have noted, the effects of different methods of cutting hedges have been reviewed (MacLean 1992), but current information is driven from experience and observational

studies rather than from experimental evidence. Acceptable management options could therefore include different cutting regimes for each hedge i.e. small branch cycle (3 to 10 years) for shrub species, coppicing (8 to 30 year cycle) for coppicing species and the tree cycle (30 to 150 years) for high trees. Pollarded trees can be managed with the traditional pollarding technique (see Reif and Schmutz 2001). The cycle lasts 8 to 15 years depending on species and growth rate ensuring the surviving of the tree and allowing periodically sunlight to neighboring woody species. All these cutting practices are aimed to have different growth forms for one or more woody species.

Increasing the area of the hedgerow is a recommended practice to enhance woody species diversity. Habitat availability (i.e. hedgerows, woods), at a range of spatial scales, has been greatly reduced where cultural intensification has affected agricultural landscapes (Benton et al. 2003). The development of many planning tools proposing hedgerow requalification and plantation (Mannino et al. 2001) deriving from the institution of Agenda 2000 in 1999 (E.C. 1999) has been a way to increase the area of existing hedgerow systems. Extending hedgerow length connecting two or more hedges can be one of the possible solutions. Another way to increase hedgerow area is extending their width, intended as maximum canopy width. To achieve this goal, one can leave grassy margins along the hedge without trimming or cutting the vegetation, allowing spontaneous regeneration of tree species in the margins. Moreover new grassy strips of variable widths can be created around all the field boundaries. Finally the thinning technique (Reif and Schmutz 2001) to maintain the right stem density of hedgerows can also be recommended. This technique helps to avoid an overly high basal area values that can negatively influence woody species richness.

5. Conclusions

This study identified three important hedgerow features, i.e. hedgerow cultural system, area and basal area that can be easily shaped by appropriate management practices to reach a defined conservation target, such as increased native woody species richness. According to these results the following practices can be recommended to enhance native woody species richness:

- (a) converting high single-storied and low single-storied to multi-storied hedgerow cultural systems;
- (b) increasing hedgerow length and/or width;
- (c) controlling the values of basal area

Agro-environmental schemes should therefore support these hedgerow management practices aimed at increasing woody species richness in the rural landscape. Future work should include silvicultural studies and tests designed to obtain detailed information regarding the optimal thinning and conversion techniques.

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