Are the ancient forests of the Eastern Po Plain large enough for a long term conservation of herbaceous nemoral species?

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Abstract

We analysed the effects of patch configuration and site history on vascular plants in ancient forests of the Eastern Po Plain, documented back to 1740. Despite their reduced size, all the forests are part of Natura 2000 Network and significantly contribute to the maintenance of a threatened habitat and support biological diversity of the Continental biogeographic region. The presence of some functional ecological plant species groups was correlated with patch configuration and age. Habitat quality, in terms of suitability for forest species, was found to be important in explaining the presence of species of high conservation value, but patch age (as an indicator for habitat quality) played a major role too. For core forest species, patch area is a redundant variable in explaining species richness relative to habitat quality and patch age and the extinction of specialists seems to occur mainly in a deterministic way. Even small forest fragments can be very important for maintaining plant species diversity, at least if they are of high habitat quality and if the forest management is appropriate. However, to achieve a long term conservation, management plans should also aim at an improvement of the anthropogenic matrix surrounding forest remnants.

Keywords: *Forest management, functional-ecological groups, habitat quality, patch configuration, patch history*

Introduction

From a historical point of view, large-scale deforestation processes in Europe took place from Neolithicum onwards, with the alternation of forest clearance phases followed by agricultural abandonment and spontaneous reforestations (Hermy & Verheyen 2007). The extent of the plain woodlands, which originally covered a large portion of the landscape, is at present strongly reduced and often only small remnants, spatially isolated, are left, with important consequences on habitat and species conservation. Habitat fragmentation may be considered one of the most important causes of biodiversity decline (Henle et al. 2004; Hanski 2005) and it is recognized as a primary topic in ecological research (Haila 2002; Fischer & Lindenmayer 2007). Fragmentation events, including loss of habitat, both in area and quality, increasing of edge effect and spatial isolation, involve consequences at different levels, from genetic flow to demographic structure of populations of species and ecosystems function,

ultimately leading to a reduction in forest species richness by increasing the extinction risk of local populations and reducing colonization of isolated fragments (Saunders et al. 1991; Bascompte & Rodríguez 2001). Species such as forest floor species of ancient forests (''ancient forest species'', *sensu* Hermy 1994), suffer increased extinction probability because of plant traits linked to their biological and ecological features. These characteristics ensue from adaptation to stable environment, supporting species with slow growth, stress tolerant strategy, early and short flowering, vegetative propagation, heavy seeds and transient seed bank (Davies et al. 2000; Jacquemyn et al. 2001; Verheyen et al. 2003). The local extinction of ancient forest species further increases for their limited dispersal power in space, which in turn leads to low recolonization ability from adjacent fragments (Honnay et al. 2005; Matlack 2005) making the so-called ''rescue effect'' impossible (Piessens et al. 2005). The long term persistence of reduced and isolated plant populations is linked mostly to vegetative reproduction and per-

ennial life cycles, so that their vulnerability can be hidden by a phenomenon called "extinction debt" (Tilman et al. 1994; Hanski & Ovaskainen 2002; Ovaskainen & Hanski 2002). After a perturbation, communities head for a process of "relaxation" (Tilman et al. 1994; Gonzales 2000), i.e. changes occurring to a community reach a new equilibrium after an environmental disturbance and, until the conclusion of this process, forest patches have an extinction debt. This means that during the relaxation time the slow species are expected to become extinct (Helm et al. 2006; Vellend et al. 2006) so that, the reaching of a new equilibrium implies a time-delayed declining of species richness, even if there is no evidence of further environmental change. Despite its high relevance it is so far a neglected aspect of the impact of global change on biodiversity and no guidelines are yet available to study it empirically (Kuussaari et al. 2009). Therefore, extinction debt can easily remain unnoticed but it should be taken into account in conservation planning.

These processes even apply to the Eastern Po Plain landscape: urban development caused a gradual destruction of the original natural habitats, in particular of the temperate forests which, from the Bronze Age, widely covered the low Venetian Plain, as palaeoenvironmental investigations suggest (Miola et al. 2006). The heavy human impact has forced woody vegetation in forest islands surrounded by a matrix typically composed of towns and arable crops (wheat, maize), very poor in hedgerows or other connecting elements.

Historical resources allow us to define our forests as "ancient forests" (Peterken 1981; Hermy et al. 1999; Hermy & Verheyen 2000), i.e. forests that have existed continuously since at least a specified date. Date differs between countries and studies and it is selected on the availability of information: e.g. Peterken (1974) suggested 1600 for Great Britain, Jacquemyn et al. (2001) 1770–1800 for Belgium, Lawesson et al. (1998) 1789 for Denmark, Grashof-Bokdam & Geertsema (1998) 1850 for Netherlands. The concept of ancient forests differs from that of old-growth forests. Even if there is a certain ambiguity on the definition of old-growth forests (Gilg 2004; Spies 2004), which are often considered as synonymous of "natural" forests, according to Peterken (1996) we refer to old-growth forests as undisturbed ecosystems, unaffected by relevant human impact since long time. Many studies have been carried out in Italy both in Mediterranean (Piovesan et al. 2005; Burrascano et al. 2008; Blasi et al. 2010; Marchetti et al. 2010) and Temperate context (Motta 2002; Burrascano et al. 2009; Digiovinazzo et al. 2010) and actually all of them refer to high natural aspects. On the contrary, the sites investigated in the present study have been traditionally used for timber production (Susmel 1994; Zanetti 1985), subjected to coppicing and even clear cutting during the Second World War, but the land cover type has never been changed. Historical land-use maps in combination with written sources and land registers (in particular, the Contarini cadastre) document the Venetian forests back to at least 1740.

Despite their reduced size, all the forests are part of Natura 2000 Network, since they have been identified as Sites of Community Importance or/and Special Protection Areas. These sites significantly contribute to the maintenance of a deeply threatened habitat and support biological diversity of the Continental biogeographic region. In fact, although few in number, fragmented and small in area, these forests are of high conservation value because they represent the last examples of the natural potential vegetation of the Eastern Po Plain and are the last remaining refuges for many species, both of fauna and flora, in the highly anthropogenic plain. Their floristic composition is also noteworthy; in fact, thanks to their unique geographical position they show the co-occurrence of Temperate-Continental species (such as *Carpinus betulus* L., *Brachypodium sylvaticum* s.l., *Geranium robertianum* L., *Quercus robur* L. ssp. *robur*), Mediterranean (*Tamus communis* L., *Ruscus aculeatus* L.) and Balkanian elements (*Lamium orvala* L., *Fraxinus angustifolia* Vahl ssp. *oxycarpa* (Willd.) Franco & Rocha Afonso).

Despite their great importance, we lack complete and updated information on communities' structure and function and on their floristic composition: a review of the available literature revealed only articles on single woods (Chiesura Lorenzoni et al. 1974; Caniglia 1981; Zanetti 1995) or incomplete and obsolete census (Zanetti 1985).

As clearly stated in the Directive 92/43/EEC, in each designated area, Member States have to implement all the necessary measures to pursue a "favourable status of conservation" of natural habitats and their typical species. So, the knowledge of the present status and of the responses of ecosystems and their components, such as forest floor species, to environmental pressures and threats is the main basis to define conservation measures involving appropriate management plans, as asked by Art. 6 of the Habitat Directive.

Hence, this work aimed to (1) collect up-to-date data on floristic composition of forest remnants; (2) verify how habitat configuration, particularly the surface, quality and history, is important in supporting plant species' richness and quality.

The overall aim of the study was to achieve a better understanding of spatial and temporal processes ruling structure, functions and dynamics of these very small and highly fragmented forest remnants in

order to hypothesize management and restoration strategies for biodiversity conservation.

Materials and methods

Site description

The investigated sites represent the totality of the relict plain forests of Veneto Region. They are located in the Eastern part of the Po Plain, four of them (Cessalto, Cavalier, Gaiarine and Mansuè) in Treviso District, and three (Lison, Zacchi and Carpenedo) in Venezia one (Figure 1). This region is characterized by the presence of an extensive agricultural, industrial and urbanized landscape. Bioclimatic classification (Rivas-Martínez 2004) shows a Temperate type, Supratemperate thermotype and humid ombrotype horizons, with a mean annual temperature of 13–14°C, low winter (0°C) and high summer (24°C) values. Mean annual

rainfall is cs. 900 mm, with maximum precipitation in the spring-autumn season and a minimum in summer (ARPAV 2008). The whole area shows a geomorphologic aspect of Holocenic plain, with alternation of humps and depressions, crossed by a drainage network deriving from the rivers historically moulding the landscape with erosive and depositional actions: Brenta (Carpenedo Wood), Piave (Cessalto, Cavalier, Gaiarine and Mansuè Woods) and Tagliamento (Lison and Zacchi Woods). Limestone-dolomitic lithologies prevail (Muscio 2001), soils are Inceptisols with a fine texture (usually silty clay), poorly drained and with moderate to low permeability (Bini et al. 2009), so that they are often saturated with water in one or more layers within 100 cm of the mineral soil surface. The pH of upper horizons is always sub-acid (6–6.5) (Bini et al. 2009). The variations of permeability in the sequence of the clastic alluvial deposits bring about the so called "spring belt", which ensures a good water availability
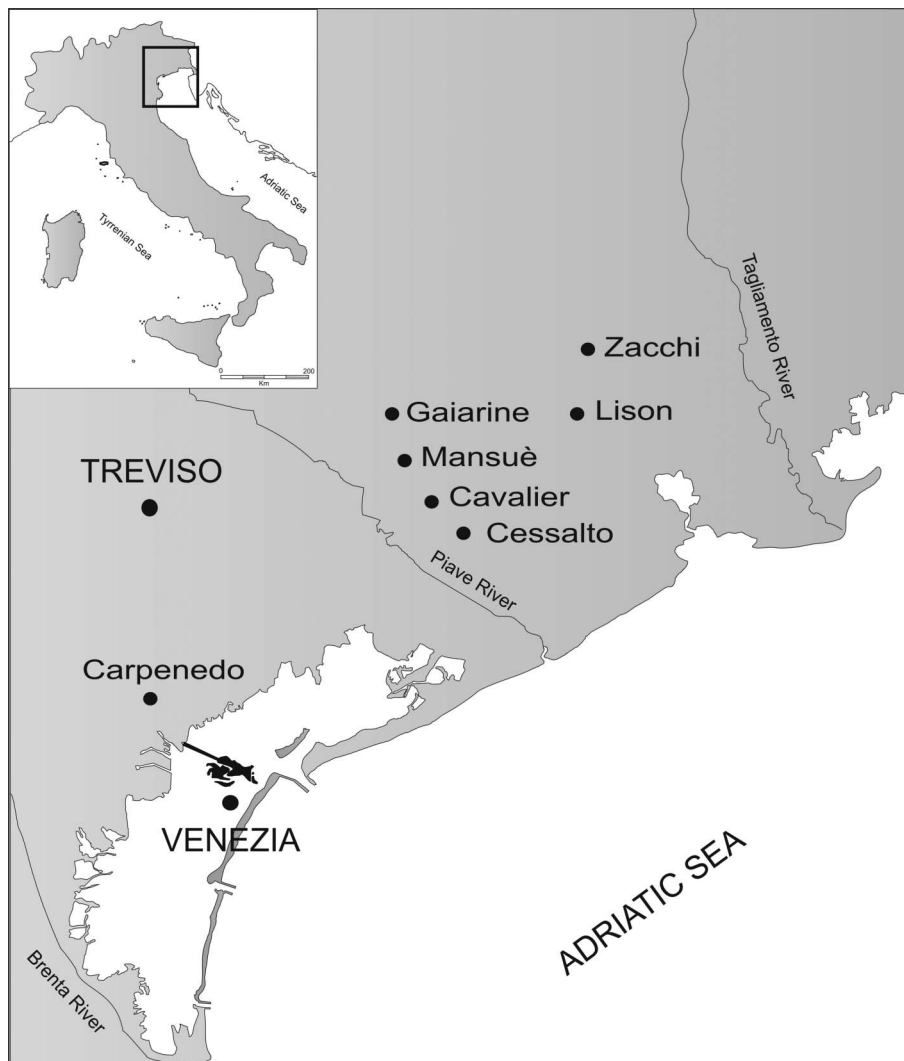

Figure 1. Location of forest patches in the study area corresponding to the eastern part of Venetian Po Plain (Treviso and Venezia Districts).

to this area supplied by a discontinuous system of water tables, 1–2 m deep.

The studied forest patches had a similar history but nowadays they differ in terms of surface, shape, intensity and time from last fragmentation, i.e. the time from the last loss of surface. The woods are very small in size ranging from 0.75 ha (Zacchi Wood) up to 27.55 ha (Cessalto Wood). Six of them are clustered (mean distance 13 km), the last (Carpenedo Wood) is scattered (minimum distance from the closest, 36 km). As fragmentation brings about deep ecological changes in the remnants, involving consequences from the structure of populations of species to the ecosystems functioning, we can describe the time from the last loss of surface as the age of the newly created fragments, which thus varies from 30 (i.e. the last loss of surface occurred 30 years ago) to 110 years. All woods are surrounded by an agricultural matrix apart from Carpenedo and Cessalto Woods which are embedded in a suburban area.

All the forests are crossed by a network of tracks, sometimes very dense and strictly interconnected. Usually they are narrow and shady, with continuous tree foliage cover, sometimes they are wide and open, with herbaceous vegetation in the central strip of the path which can be periodically mown (e.g. Cessalto and Mansuè Woods).

The forests belong to the *Asparago-Quercetum roboris* (Lausi 1966) Marinček 1994 of the alliance *Erythronio-Carpinion* (Horvat 1958) Marinček in Wallnöfer et al. 1993; in the deeper places some aspects referable to *Alno-Quercion roboris* Horvat 1938 (*Leucojo-Fraxinetum* s.l.) can be found. According to Natura 2000 classification they belong to the habitat 91L0 (Illyrian oak-hornbeam forests (*Erythronio-Carpinion*)) with some aspects of 91F0 (Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)) (Poldini et al. 2009; Buffa & Lasen 2010).

Data collection and analysis

With the aim of carrying out a species list for each surveyed unit, floristic data were collected by intensive investigations during the whole vegetative period of 2008–2009 and in Spring 2010. Furthermore, in order to detect the ancient forest species patch occupancy in the seven sites, a random sampling design was used to fix 80 plots (25 × 25 m). As most of the authors assume ancient forest species to be associated with the interiors of forests, plots were distributed proportionately to the woods surface to cover approximately the 50% of core area surface of each remnant, avoiding the zone of transition, from the edge, 50 m inwards (Ries et al.

2004). Survey site delimitation was very easy because all forested patches have sharp edges and differ deeply from the surrounding landscape. Floristic collection covered all habitats inside the sites, therefore species of grasslands and wet meadows have been included in the complete check-list, even if they are exclusive of tracks and paths. Taxa nomenclature follows Conti et al. (2005) and Conti et al. (2007).

To analyse the influence of fragmentation on species richness two approaches were adopted: first we applied species/area analysis using the total species richness and then we focused on the different effects due to the ecological characteristics (traits) of the forest plant species. Except for total species/area analysis, we did not count species strictly linked to the paths (belonging to the classes *Molinio-Arrhenatheretea* R. Tx. 1937 em. R. Tx. 1970 and *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941) and rarely occurring inside the forest.

To identify possible functional groups in terms of patch occupancy patterns linked to the plant traits, a Principal Component Analysis (PCA) from covariances was carried out, using the package Syn-tax 2000 (Podani 2001). For all species, except those linked to the paths and exotic species, life history traits were collected from available bibliographic sources and on-line archives (Klotz et al. 2002; Fitter & Peat 2004; Kleyer et al. 2008), based on morphology (life form; Pignatti 1982), floral and reproductive biology (type of reproduction, pollen vector, dispersal mode; among others, Honnay et al. 1998; Verheyen & Hermy 2001; Vittoz & Engler 2007), and ecological strategy (according to Grime 1979; Grime et al. 1988). The PCA was applied to the binary matrix of traits states or attributes × species (25 traits states × 181 species). Traits (Table I) were chosen for their significance in plant community assembly processes in fragmented landscapes (Davies et al. 2000; Dupré & Ehrlén 2002; Verheyen et al. 2003; Hérault & Honnay 2005), i.e. traits associated with the response of plants to the loss of habitat and linked environmental changes (response traits) (Lavorel & Garnier 2002).

Patch configurations were derived from digitised geo-referenced aerial photographs, using Arc-View GIS software and Fragstat 3.3 (McGarigal et al. 2002). In particular GIS analysis tools were used to calculate the following landscape metrics: present patch area, perimeter, isolation (by proximity index) (Gustafson & Parker 1994) and shape, by means of shape index (Patton 1975). Patton's shape index was chosen, among others, because it measures the complexity of patch shape compared to a standard shape (square or almost square) of the same size, thus alleviating the size dependency problem. Past patch area and time from last loss of surface (i.e. age) were used, as additional variables, selected on the

Table I. List of functional traits and their attributes used to perform the Principal Component Analysis (25 attributes × 181 species). Percentage of missing values is reported.

Plant traits	Acronyms	Attributes	Missing values (%)
Life form	LF	P = Phanerophyte; NP = Nanophanerophyte; H = Hemicryptophyte; G = Geophyte; T = Therophyte	none
Type of reproduction	TR	s = by seed/spore; sv = by seed and vegetative; ssv = mostly by seed, rarely vegetatively; vvs = mostly vegetatively, rarely by seed	1.5
Pollen vector	PV	in = insects; se = selfing; w = wind	1.1
Dispersal mechanism	DM	AN = Anemochory; AU = Autochory; DY = Dyszoochory; EN = endozoochory; EP = Epizoochory; MY = Myrmecochory	none
Ecological strategy types	ST	C = competitors; R = ruderals; ST = stress-tolerators; CSR = competitors stress-tolerators ruderals; CS = competitors stress-tolerators; CR = competitors ruderals; SR = stress-tolerators ruderals	0.3

basis of their possible influence on species' presence and persistence. As studied remnants underwent the last loss of surface in different periods we can assume them as a chronosequence which allows us to follow and infer floristic composition changes in time. All these variables were used to perform a regression analysis with STATISTICA software (StatSoft 2001). As habitat configuration and site history could influence forest structure, we related them not to the total species richness but to the relative weight of the different ecological groups that emerged from PCA.

Landscape metrics and the floristic composition in terms of functional-ecological groups, have also been used to perform a Principal coordinates Analysis (PCoA) (resemblance coefficient: similarity ratio), to explore the main trends of variability among the remnants.

As we lack exhaustive past information and time series data on species and habitats, to evaluate indirectly the extinction debt we estimated the suitability of the patches, that is, the fitness after fragmentation events, for the core forest species.

To assess the suitability, we relied on Ellenberg indicator values to calculate a habitat-unsuitability index (h_{ki}) (Verheyen et al. 2004). In this study, we used Ellenberg indicator values revised for Italy (Pignatti et al. 2005). According to Verheyen et al. (2004) for each focal species k (each ancient forest species) in every patch i, we calculated the index as follows:

$$h_{ki} = |N_k - MIV\_N_{i(J \neq K)}| + |R_k - MIV\_R_{i(J \neq K)}| + |F_k - MIV\_F_{i(J \neq K)}|$$

where N_k, R_k, and F_k are the indicator values for soil nitrogen, acidity, and humidity, respectively, for the focal species k; $MIV\_N_{i(J \neq K)}$, $MIV\_R_{i(J \neq K)}$, and $MIV\_F_{i(J \neq K)}$, are the means of the indicator values of all species j (not including k) present in the patch.

High h_{ki} values indicate that the soil preferences of the other species in patch i are different to those of the focal species k, and consequently that the environmental conditions in the patch are unlikely to be suitable for the focal species. So, we can assume that species with high h_{ki} values are still present because of their slow responses to habitat perturbations but they are prone to local extinction.

Results

Flora

A list of 257 vascular plant species was compiled (Stoppa et al. 2012), not restricted to forest species, but including edge and path species. The woody vegetation is dominated by *Quercus robur*, *Carpinus betulus* and *Fraxinus ornus* L.. The shrub and vines layer is mainly composed of *Hedera helix* L., *Euonymus europaeus* L., *Ligustrum vulgare* L., *Cornus sanguinea* L., *Crataegus laevigata* (Poir.) DC., *C. monogyna* Jacq. and *Lonicera xylosteum* L., The most common species of the herbaceous layer are all perennials such as *Anemone nemorosa* L., *Arum italicum* Mill., *A. maculatum* L., *Lamium orvala*, *Lamium galeobdolon* L., *Polygonatum multiflorum* (L.) All., *Ranunculus auricomus* aggr. (*R. palaeoeuganeus* Pign.) and *Viola reichenbachiana* Jordan. ex Boreau. Non-native species most commonly found are *Prunus cerasifera* Ehrh., *P. laurocerasus* L., *Robinia pseudoacacia* L. and *Laurus nobilis* L.. Despite these common elements, the surveyed woodlands show remarkable differences in terms of species richness which ranges from 70 to 170 species.

Functional traits

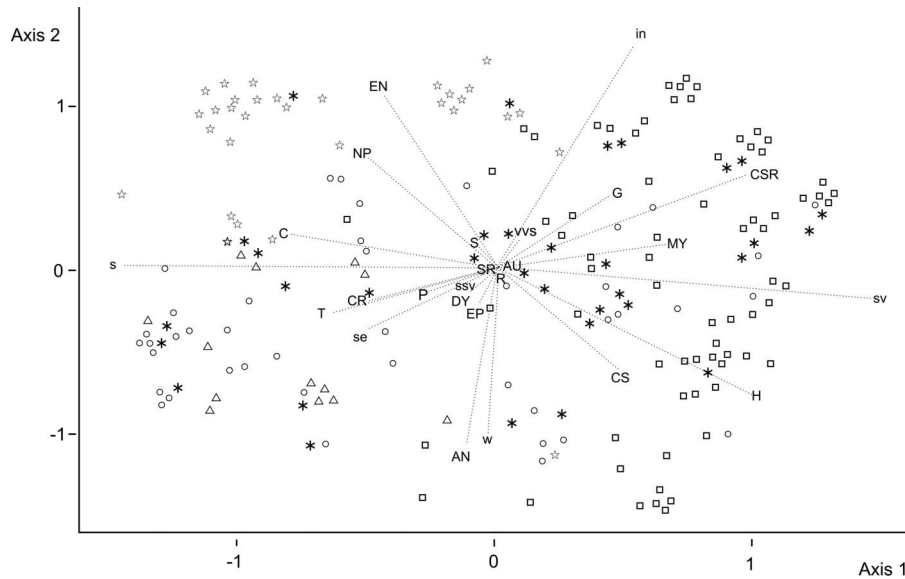Principal Component Analysis shows the main relationships among species (Figure 2, Table II).

Figure 2. Principal Component Analysis of species and traits attributes (25 attributes × 181 species). Symbols refer to emerged groups: triangle: woody forest species; square: herbaceous core species; star: mantle species; asterisk: edges species; circle: ruderal species). Grasslands and non-native species were not used in the analysis. Attributes acronyms: Life forms: P = Phanerophyte; NP = Nanophanerophyte; H = Hemicryptophyte; G = Geophyte; T = Therophyte; Type of reproduction: s = reproduction by seed/spore; sv = reproduction by seed and vegetative; ssv = reproduction mostly by seed, rarely vegetatively; vvs = reproduction mostly vegetatively, rarely by seed; Pollen vector: in = insects as pollen vector; se = selfing; w = wind as pollen vector; Dispersal mechanism: AN = Anemochorous; AU = Autochorous; DY = Dyszoochorous; EN = Endozoochorous; EP = Epizoochorous; MY = Myrmecochorous; Ecological Strategy Types: C = competitors; R = ruderals; ST = stress-tolerators; CSR = competitors stress-tolerators ruderals; CS = competitors stress-tolerators; CR = competitors ruderals; SR = stress-tolerators ruderals. Cumulative percentage variance of axis 1 and 2: 36%.

The first PCA axis, accounting for approximately 20% of the total variance, is mostly correlated to the type of reproduction, and separates species, both woody and herbaceous, which reproduce by seeds, on the left side, from species that reproduce mostly vegetatively or as a frequent alternative. The second PCA axis, accounting for approximately 16% of the total variance, refers to pollen and seed vectors, classifying species into two major groups, from abiotic vectors (wind) to biotic ones.

Others traits used to perform the PCA successfully separate smaller groups. Therefore, on the left side, emerges the group of phanerophytes and nanophanerophytes, which reproduce by seeds and are mostly competitive species (*sensu* Grime 1979). They can be divided into two groups according to their pollen vector and dispersal mechanism: trees use mostly the wind, both for pollen and seeds, while for nanophanerophytes animals are important pollen and dispersal vectors (mostly endozoochory). Woody species are mixed with short cycle species with which they share reproduction via seeds and the preference for abiotic vectors, but they can be easily differentiated on the basis of strategies, as short cycle species are mostly ruderal or competitive-ruderal. While these three groups were quite easily identifiable, a finer separation among long cycle herbaceous species was only possible introducing another variable, i.e. the phyosociological affinity, as given in

Ellenberg et al. (1992); Grabherr & Mucina 1993; Mucina et al. (1993a; 1993b) and Poldini et al. (2002). Classes involved were *Querco-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937 and *Alnetea glutinosae* Br.-Bl. et R. Tx. ex Westhoff et al. 1946, for core forest species; *Trifolio-Geranietea* T. Müller 1961 and *Epilobietea angustifolii* R. Tx. et Preising in R. Tx. 1950 for tall-forbs communities of edges; *Artemisietea vulgaris* Lohmeyer et al. in R. Tx. 1950 and *Stellarietea mediae* R. Tx., Lohmeyer et Preising in R. Tx. 1950 for species of anthropogenic, ruderal communities.

Following this classification, perennial herbaceous species could be separated in three quite homogeneous groups. Core forest species show some common traits, such as a strong vocation for vegetative reproduction (sv and vvs) and ants as preferential dispersal agent. Anyway, they occupy two different temporal and spatial niches: nearly 50% are small spring geophytes, CSR strategists, with entomophilous pollination. The other 50% is represented by higher hemicryptophytes, later flowering, with CS strategy. This second group is more heterogeneous and shares some traits (i.e. wind as pollen vector and dispersal agent) with other groups, due to the presence of ferns and grasses. Ruderals and edge species do not show an evident and characterizing set of traits but they split over other groups. As already seen, only ruderals perform a

Table II. Percentage distribution of each trait attributes in the groups emerged from PCA applied to the binary matrix of attributes × species (25 attributes × 181 species).

Traits acronyms	Traits attributes	Wody forest species	Ancient forest species	Mantle species	Edges and clearings species	Ruderal species
LF	P	92.31	0.00	6.45	0.00	0.00
	NP	7.69	0.00	83.87	3.33	0.00
	H	0.00	54.17	3.23	60.00	52.27
	G	0.00	43.06	3.23	13.33	11.36
	T	0.00	1.39	0.00	23.33	36.36
TR	s	46.15	19.44	54.84	33.33	59.09
	ssv	46.15	2.78	9.68	6.67	4.55
	sv	7.69	73.61	32.26	53.33	29.55
	vvs	0.00	8.33	3.23	6.67	6.82
PV	in	30.77	66.20	87.10	75.76	9.09
	se	7.69	9.86	6.45	15.15	31.82
	w	61.54	22.54	6.45	9.09	27.27
	Missing values	0.00	1.41	0.00	0.00	2.27
DM	AN	84.62	20.83	9.68	43.33	54.55
	AU	6.25	11.11	0.00	10.00	6.82
	EN	7.69	18.06	83.87	20.00	9.09
	EP	0.00	19.44	3.23	16.67	18.18
	MY	0.00	34.72	0.00	3.33	4.55
	DY	0.00	0.00	0.00	0.00	4.55
	Missing values	0.00	0.00	3.23	6.67	2.27
ST	C	100.00	4.17	87.10	43.33	27.27
	CR	0.00	1.39	0.00	20.00	36.36
	CS	0.00	48.61	6.45	10.00	4.55
	CSR	0.00	47.22	3.23	23.33	18.18
	S	0.00	2.78	3.23	0.00	0.00
	R	0.00	0.00	0.00	0.00	13.64
	SR	0.00	0.00	0.00	3.33	0.00

Notes: Attributes acronyms: Life forms (LF): P, Phanerophyte; NP, Nanophanerophyte; H, Hemicryptophyte; G, Geophyte; T, Therophyte; Type of reproduction (TR): s, reproduction by seed/spore; sv, reproduction by seed and vegetative; ssv, reproduction mostly by seed, rarely vegetatively; vvs, reproduction mostly vegetatively, rarely by seed; Pollen vector (PV): in, insects as pollen vector; se, selfing; w, wind as pollen vector; Dispersal mechanism (DM): AN, Anemochorous; AU, Autochorous; DY, Dyszoochorous; EN, Endozoochorous; EP, Epizoochorous; MY, Myrmecochorous; Ecological Strategy Types (ST): C, competitors; R, ruderals; ST, stress-tolerators; CSR, competitors stress-tolerators ruderals; CS, competitors stress-tolerators; CR, competitors ruderals; SR, stress-tolerators ruderals.

certain polarization, due to the short life cycle and a ruderal strategy (R and CR), linked to the frequent disturbance. Dispersal vectors (myrmecochory versus anemochory) and life strategy (stress-tolerant versus competitive-ruderal) (Table II) appear as major discriminants relative to ancient forest species. Edge species show the broadest ecological amplitude: they use mostly insect for pollination, while for seeds dispersal they use both wind (40%) and zoochory (36%); they reproduce by seeds but many can spread vegetatively. Relative to core species, they can be differentiated according to their strategy, being mostly competitive or competitive-ruderal.

Therefore, according to the emerged groups, 44.74% of the detected species are true forest species (of which 27.62% are ancient forest species and 12.06% are species of the mantle), the natural component of a forest, i.e. specialists; the rest is made up of "alien" species, that is, species not strictly associated with nemoral context, i.e. generalists.

The groups that emerged from PCA allow us to better describe differences in forest species composition and structure. As the regional pool of woody forest species is composed by a low and finite number, this component does not vary among forests ($\chi^2 = 1.89$, $p = 0.9$), but what does vary is its proportional weight, growing from larger to smaller woods. The forest floor component shows two different trends: while core forest species express a non-linear tendency ($\chi^2 = 22.03$, p = 0.001), edge species ($\chi^2 = 17.84$, $p = 0.006$) and ruderals ($\chi^2 = 45.08$, $p = 0.001$) grow up from smaller to larger forest patches.

Species-area relation

The correlation between total floristic richness and patch area, both log transformed, is positive and highly significant ($R^2 = 0.71$; p < 0.05) (Table III), to indicate that the smaller forests are, the fewer species they contain.

Table III. Regressions of the logarithm of the number of species of the different groups (y) on the logarithm of the present and past patch area (x) (log $y = z$ log x + c).

	Species group	z	s.e. (z)	c	s.e. (c)	R^2	Sign.
Present patch area	All species	0.218	0.062	1.883	0.053	0.710	0.017*
	Woody forest species	0.105	0.054	0.815	0.046	0.427	0.111
	Ancient forest species	0.188	0.090	1.383	0.077	0.465	0.091
	Mantle species	0.025	0.037	1.334	0.031	0.083	0.529
	Edge species	0.443	0.065	0.753	0.055	0.902	0.001***
	Ruderal species	0.678	0.167	0.564	0.142	0.766	0.009**
	Non-native species	−0.019	0.110	1.013	0.097	0.005	0.874
Past patch area	All species	0.392	0.117	0.861	0.352	0.692	0.02*
	Woody forest species	0.180	0.103	0.348	0.309	0.380	0.14
	Ancient forest species	0.321	0.173	0.552	0.521	0.407	0.123
	Mantle species	0.049	0.067	1.205	0.203	0.095	0.501
	Edge species	0.795	0.132	−1.323	0.399	0.878	0.001**
	Ruderal species	1.229	0.309	−2.651	0.930	0.760	0.01*
	Non-native species	−0.014	0.208	1.043	0.628	0.001	0.946

Note: sign., level of significance (* ≤ 0.05–0.01; ** ≤ 0.01–0.001; *** < 0.001).

The species-area relationship shows a changeable significance if we focus the analysis on the single groups of species that emerged from PCA. The highest R^2 value is shown by edge species with a trend similar to those of ruderal species, which are strongly related to the area. No relationship is pointed out for non-native species and mantle species, which are equally distributed in all woods. Forest species show an intermediate relationship with area both for the woody component and ancient forest species.

Linear regression of species number (log) on the past patch area (log) shows similar trends (Table III). Species number increases with increasing patch area for both specialist and generalist species, and hence, also for all species combined. To highlight differences, z is the key value, which, in this case ranges from −0.014 to 1.23. z-Value traces the slope of the line, so that, the greater the value of z, the greater the increase of species predicted for any given increase in habitat area (Lewis 2006). According to this view, species most favoured during the relaxation time following the fragmentation event are generalists, such as ruderals and edge species, while core species do not show a higher relationship with past patch area, i.e. to the state prior to habitat loss.

Patch configuration and site history

To evaluate the effect of patch configuration on the floristic assessment, structural landscape metrics have been related to the groups that emerged from PCA.

The shape index ranges from 1.0 for forests with the most regular shape (Zacchi and Carpenedo Woods), up to 1.5 for the most elongated one (Cessalto), that is, smaller forest patches have a more compact shape than larger one. Even proximity shows a broad variation, with six forests more or less clustered (mean Proximity index = 0.4, s.d. 0.16) and one definitely scattered (Carpenedo Wood, Proximity index = 0.04).

As a general pattern, present landscape parameters are not likely to affect the woods' structural composition so much (Table IV), but again emergent groups answer differently.

The forests' shape has no influence on the occurrence of all ecological groups, except edge species whose number and density are naturally driven by irregular forms and longer perimeters. The relationship is positive and the significance is high only for this group. Moreover, the most part of the groups show a negative trend, while edge and ruderal species grow up with a steep slope.

Only specialists are favoured by patch proximity, in fact ancient forest species are strongly affected by the closeness of patches and their proportional weight rapidly increases (Table IV).

The time from the last fragmentation, i.e. the age of fragments, again does not have a univocal trend, with specialists showing basically a decrement and generalists an increment. Assuming remnants as a temporal sequence, the regression analysis allows us to infer a loss in time of the high quality species and a parallel increase of low quality species.

A part from the detailed significance, the relationships show a general rule, with specialists following a negative trend, i.e. they are negatively influenced by the complexity of the patch shape, isolation and age; on the contrary, generalist species, typical of edges, clearings and disturbed habitats, show a positive trend.

Age, particularly, emerges as an explanatory variable (Table V). The observed t-value (2.02) exceeds the critical value (Student's t-distribution for 10 d.f. = 1.81) only for 90% confidence interval and

Table IV. Regressions of percent of species belonging to the different groups (y) on the value of the patch shape index (x), proximity index (x) and age (x) ($y = bx + c$).

	Species group	z	s.e. (z)	c	s.e. (c)	R^2	Sign.
Shape index	All species	99.358	68.546	−5.660	83.001	0.296	0.207
	Woody forest species	−1.651	3.917	9.268	4.743	0.034	0.691
	Ancient forest species	−5.972	15.206	37.866	18.412	0.030	0.71
	Mantle species	−17.162	10.458	41.859	12.663	0.350	0.161
	Edge species	12.921	4.284	4.403	5.187	0.645	0.029*
	Ruderal species	146.960	10.783	6.007	13.057	0.271	0.231
	Non-native species	−11.554	6.195	23.547	7.502	0.410	0.121
Proximity index	All species	−31.727	44.433	127.74	24.705	0.092	0.507
	Woody forest species	2.265	2.038	6.259	1.133	0.198	0.317
	Ancient forest species	17.486	4.069	22.747	2.262	0.787	0.007**
	Mantle species	−0.730	7.399	21.646	4.114	0.002	0.925
	Edge species	0.064	4.107	11.036	2.283	0.001	0.988
	Ruderal species	−7.204	6.450	14.870	3.586	0.199	0.315
	Non-native species	−3.002	4.406	11.082	2.450	0.085	0.526
Age	All species	0.545	0.428	78.260	30.389	0.245	0.259
	Woody forest species	−0.037	0.017	9.683	1.231	0.479	0.084
	Ancient forest species	−0.139	0.069	39.689	4.902	0.450	0.099
	Mantle species	−0.069	0.072	25.721	5.108	0.154	0.384
	Edge species	0.028	0.041	9.263	2.974	0.084	0.529
	Ruderal species	0.107	0.059	4.683	4.195	0.398	0.128
	Non-native species	−0.030	0.046	11.663	3.316	0.077	0.545

Notes: sign., level of significance (* $\leq$ 0.05–0.01; ** $\leq$ 0.01–0.001; *** < 0.001).

Table V. Regression of percent of species belonging to specialists (woody forest species, mantle species and ancient forest species) and generalists (ruderals and edges species) (y) on the age (x) ($y = bx + c$).

Species group	z	s.e. (z)	c	s.e. (c)	R^2	Sign.
Specialists	0.096	0.176	1.634	0.313	0.056	0.609
Generalists	0.865	0.342	0.105	0.607	0.560	0.053

Notes: sign., level of significance (* $\leq$ 0.05–0.01; ** $\leq$ 0.01–0.001; *** < 0.001). (t-value: 2.02; d.f. 10 = 1.81).

is only a little below the threshold for p-level of 0.05 (t-expected = 2.22), but even if the difference between z-values is only nearly significant, it describes clear different trends of temporal variation, with specialists that remain nearly constant and generalists which rapidly grow up.

PCoA

The PCoA (Figure 3), obtained using biological and landscape metrics, helps us to identify which parameters can better predict structural composition. In support of previous results, the floristic composition and structure of the woods, expressed by the percentage of ecological groups, are substantially defined by three variables. The first axis (48.82 % of total variance) is associated with age (Spearman's rank correlation coefficient = 0.78, $p < 0.05$), area (Spearman's rank correlation coefficient = 0.78, $p < 0.05$) and total number of species (Spearman's rank correlation coefficient = 0.78, p < 0.05), while other landscape metrics such as shape and isolation show no significant correlation. Both area and age lead to a higher number of species (increasing from left to right), given mainly by an increase of ruderals (Spearman's rank correlation coefficient = 0.82, $p < 0.05$). Thus, from left to right, axis 1 can be read as a gradient of increasing floristic relaxation, highlighted by a growing contribution of ruderals and, subordinately, edge species to community composition. To test this hypothesis we calculated Spearman's rank correlation coefficients between the PCoA coordinates and the percent values of specialists and generalists inside each woods: while no correlation has been outlined for specialists (Spearman's rank correlation coefficient = −0.67, p < 0.09), the percentage of generalists comes out to be the most significant variable (Spearman's rank correlation coefficient = 0.89, $p < 0.05$). The floristic composition of older and larger woods is made up of a growing percentage of ''alien'' species, not strictly associated with nemoral context. Tracks and anthropogenic clearings, mostly present in Mansuè, Cessalto and Carpenedo Woods, creating gaps on
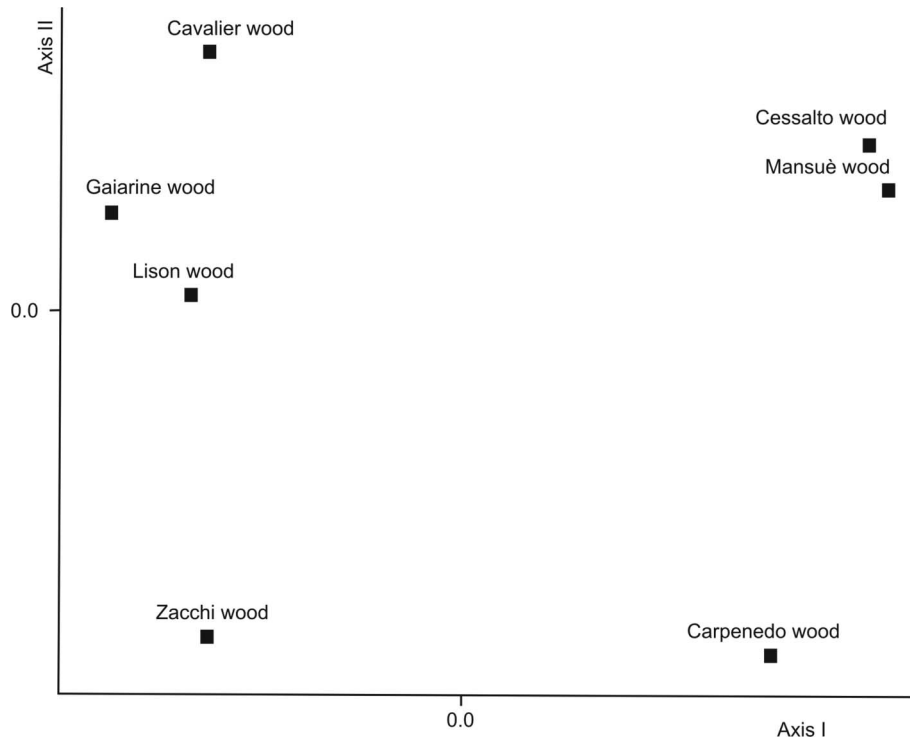
Figure 3. Principal coordinates Analysis (PCoA) of the investigated forests applied to the matrix of landscape metrics and floristic composition in terms of percentage of the groups emerged from PCA (resemblance coefficient: similarity ratio). Cumulative percentage variance of axis 1 and 2: 73.03.

the canopy, farther favour edge and ruderal species. The second axis (24.21% of total variance) exhibits a low significant correlation merely with patch area (Spearman's rank correlation coefficient $= 0.64$, $p < 0.1$), which decreases from the top downwards. Zacchi and Carpenedo Woods are two of the smallest fragments (0.75 ha and 2.77 ha respectively), but they deeply differ in age, Zacchi being the youngest (only 30 years from the last fragmentation) and Carpenedo the oldest (110 years).

Habitat unsuitability (HU) and patch occupancy

For the whole species set, HU values vary from 0.89 up to 8 and show roughly a normal distribution (Figure 4), with central values highly represented; core forest species show a narrower range, from 1.23 to 7.25 with a different values distribution: 53% of average HU values lay between 1 and 3, the remaining 47% splits up in the higher classes, with a decreasing trend. Only three species, *Polypodium vulgare* L., *Gagea spathacea* (Hayne) Salisb. and *Melampyrum pratense* L., belong to the highest class.

No linear relationship between HU values and ancient forest species percentage of patch occupancy is demonstrated (Figure 5); species with high HU values show a very low average (all woods) percen-
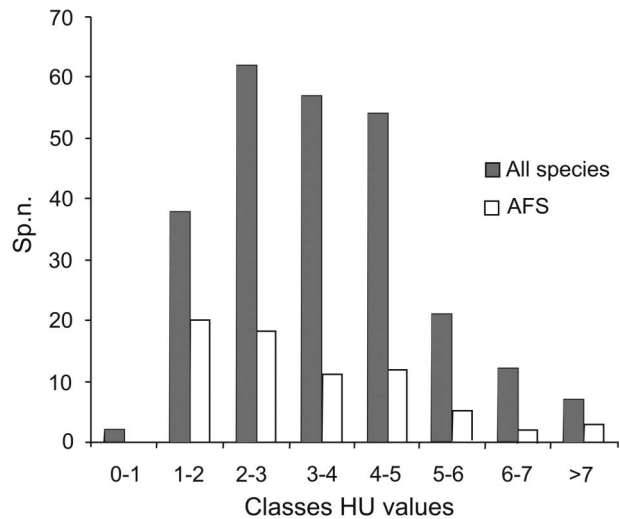

Figure 4. Histogram representing the distribution of the HU values; all species (grey), ancient forest species (white).

tage of patch occupancy (between 0 and 35%), but the opposite is not always true: species with medium HU values show very different patch occupancy and even species with low value (< 2) could express very low percentage of patch occupancy (i.e. *Carex umbrosa* Host, *Galanthus nivalis* L., *Lilium martagon* L.), being present in only one forest.

Considering only core species recorded in at least 4 forests ($n = 40$), significant ($R^2 > 0.3$) effects of

Occurrence in Forests
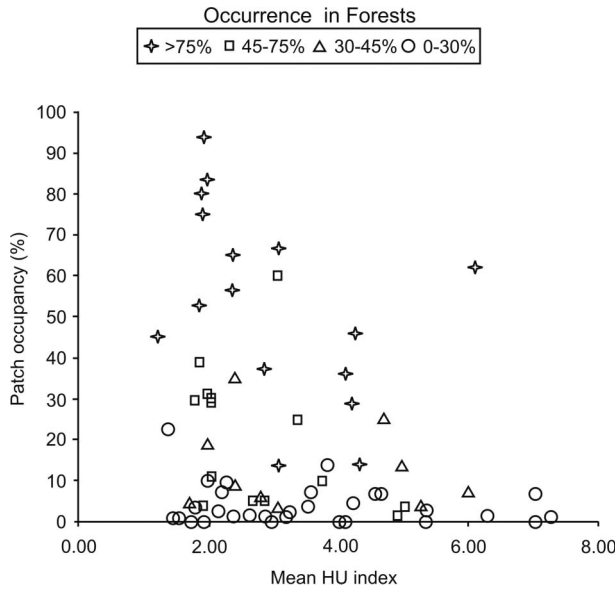
| ✦ >75% | □ 45-75% | △ 30-45% | ○ 0-30% |

Figure 5. Relationship between the mean value of patch occupancy in each wood and the mean HU values for the ancient forest species (Spearman rank correlation coefficient $= -0.22$, $p >$ 0.05, $n = 71$). Different symbols indicate the percentage of species occurrence in the seven ancient forests.

the HU on percentage of wood-specific patch occupancy were found for 18 species (45%).

Testing the effects of patch configuration and history (area, shape and age) on species-specific HU, 5 (12%), 20 (50%) and 16 (40%) species were found respectively, with either negative (area) or positive (shape and age) relationship. Therefore, HU values seem to depend mostly on shape and age. Irregular and older remnants are affected to a greater extent by matrix factors, whereas regular and younger patches seem to be less affected by the environmental changes occurring at the edges, irrespective of area.

Significant area, shape, proximity and age effects on percentage of patch occupancy were found for 5 (12%), 7 (17%), 5 (12%) and 11 (27%) species, respectively. In this case, too, the signs of the relationships were either positive (area and proximity) or negative (shape and age) and the most important independent variable affecting patch occupancy seems to be patch age.

In total, 38 species (95%) answer to one or more patch configuration variables. No relationship exists between patch occupancy and plant traits such as life forms (18 geophytes versus 20 hemicryptophytes) or strategy (18 CSR versus 18 CS; only 2 C), while dispersal mode seems to be strategic, as 20 species (52%) share myrmecochory. Only one myrmecochorous species (*Carex sylvatica* Huds.) shows a positive relationship between percentage of patch occupancy and proximity, while others are endozoochorous or anemochorous species.

Discussion

Over the past century, lowland temperate woodlands in Europe have suffered a major decline in their area due to land-use changes and currently forest species are restricted to small and isolated patches, surrounded by fields, crops and towns. Although an active reforestation policy is in place, newly established forests, originating from set-aside farmlands that were previously under intensive agricultural management, do not result in ecologically valuable forest habitats in the short term.

As a consequence, ancient forest plant species are generally confined to ancient forests which become of unavoidable importance for the conservation of plant species richness in fragmented, agricultural landscapes. As ancient forest species are excellent indicators of the ecological value of forest communities (Peterken 1974), it is of great importance to understand the processes underlying their occurrence and abundance, especially in small forest remnants.

Our results confirm the well known correlation between vascular plant species number and patch size showed by many research studies and reviews on fragmentation effects (Honnay et al. 1999a; Godefroid and Koedam 2003; Petit et al. 2004; Rosati et al. 2010).

As already pointed out (Graae & Sunde 2000; Adriaens et al. 2006), relying only on overall community measures, such as total species richness, can hide trends connected to specific components of communities: it can be expected that differences in dispersal capacity and other biological strategies among species, together with processes external to the community (i.e. habitat and landscape spatial configuration) should differently impact on distinct groups of species so leading to a non-random local community structure.

The utilization of emergent functional groups allowed us to interpret differences in the relative importance of landscape structure and local environmental conditions in terms of the ecological profile of the corresponding groups.

As a matter of fact, the relationship with current remnants area persists for most of the emergent groups, but with differential response of specialist and generalist species groups. In fact they perform different ecological strategies in terms of colonization and extinction rate, competitive ranking and ability in resources' exploitation and fitness.

These traits trace back to the general mechanisms underlying competition and coexistence via life history trade-offs (among others Nee & May 1992; Tilman 1994; Amarasekare 2003): core forest species (particularly small geophytes) are superior competitors which are fecundity-, recruitment- or

dispersal-limited, or lack the ability to exploit resource-rich conditions typical of disturbed habitats. Edge species and, especially, ruderals are inferior competitors, which, on the contrary, have high fecundity, recruitment ability or long dispersal range, being so able to colonize early successional and disturbed habitats. Thirty-four per cent of ancient forest species are dispersed by ants (myrmecochores), 37 per cent are zoochores but are mainly dispersed by species with a very small home range (Honnay et al. 2002) and only 20 per cent are dispersed easily by wind. Besides, most of these species have low competitive ability and high stress tolerance (50 per cent are stress tolerators or competitive stress tolerators *sensu* Grime 1979). Because of their traits, superior competitors cannot exploit all the new available sites and leave gaps in the habitat which are quickly occupied by inferior competitors with higher colonization ability. Edge and ruderal species in fact are mostly represented by ruderal, competitive or competitive-ruderal species (more than 60 per cent for both).

This theoretical framework, together with the outcomes of our study, drives us to highlight the importance of the area as a secondary factor relative to species-specific characteristics and habitat quality and history, as already pointed out by other recent studies on forest plant patch occupancy (Dupré & Ehrlén 2002; Kolb & Dieckmann 2005). Quality of the plant communities did not show a gradual change from larger to smaller patches, with larger patches being characterised by a higher proportion of core forest species, and both larger and smaller patches hosted rare and threatened forest species (such as *Mercurialis perennis* L., *Paris quadrifolia* L., *Ophioglossum vulgatum* L. and *Orchis purpurea* Huds.) depending on their inner quality. This means that when enough core area, i.e. suitable area, is available also small forest patches (a few ha) seem able to support valuable plant communities. So the forest fragment area appears a redundant variable and specialists patch occupancy seems mostly correlated to habitat age and to its quality, with age and quality in inverse proportion, that is, increasing age leads to decreasing quality. Patch age confirms its importance both at patch level, grouping forests mainly according to their age, and at species level, explaining growing HU and patch occupancy. This result confirms the process of relaxation and the presence of an extinction debt to be paid by all those species with the highest values of HU.

The high impact of age and, to a lesser degree, area, hide the effect of other variables. A high shape index has a positive effect on species quantity but yielding a negative effect on species quality and large tracks inside the forests act extending edge habitats and matrix effects so causing a shift in species composition, favouring generalists. Even if, in our case, there was apparently no negative effect on the number of forest core plant species, it is clear that in small forest patches an irregular shape leaves less suitable habitat for forest core species.

Even isolation shows nearly no correlation with species richness and composition since only ancient forest species seem to be supported by proximity but if we consider the correlation between species-specific patch occupancy and isolation, only endo-zoochorous and anemochorous species express a positive relationship. Moreover, current number of core species shows nearly the same correlation both with present and past area giving evidence for a possible fictitious link with proximity. Species diversity in small remnants of ancient woodlands does not decrease even after several decades of isolation (Dzwonko & Loster 1989; Honnay et al. 1999b). It may take more than 100 years to change the composition of forests and, according to Honnay et al. (1999b), after a fragmentation history almost 1000 years are required to reach a new state of equilibrium on species composition. Therefore, the ability of forest species to persist through clonal growth, responding slowly to environmental changes, could suggest that current patch occupancy reflects more truly the historical landscape.

Conclusion

Our study has pointed out a critical situation for species restricted to seminatural forests in Venetian Po Plain. Nevertheless, from a forest plant species conservation perspective and on a human time-scale, the importance of small forest patches should not be underestimated. Forest plants can persist for a very long time, even in small forests, provided that the forest management is appropriate, protecting the forest core area from severe anthropogenic disturbance. The persistence of populations depends mostly on the chance for organisms to find suitable environmental conditions, so for sessile species, relatively immobile such as forest specialist species, priority has to be given to habitat quality preservation.

This applies especially to highly fragmented habitats in an agricultural or urbanised landscape. The main conclusion of this study implies that conservation efforts have to be focused primarily on maintaining environmental quality, in terms of suitability for forest species. In the Venetian context, this mainly involves both reducing the lateral influx of pesticides and fertilisers from neighbouring agricultural land and refining forest management currently acting as a local extinction deterministic factor. Management regime, inducing unfavourable environmental conditions, can affect remnant populations dynamics and inhibit normal life cycle

finishing. The slowdown in traditional management regime, following an erroneous idea of conservation, is threatening the population dynamics of perennial forest herbs species which is strongly influenced by successional stage through the degree of canopy closure and low light conditions can suppress sexual recruitment and trigger clonal growth (Honnay & Bossuyt 2005). In turn, the opening of wide tracks inside the woods makes the penetration of generalist species easier thus changing the competitive relationships among species, via the replacement of stress tolerant species with more competitive ones.

Restoration activities should include firstly the creation of buffer zones, to minimize edge effects and to promote characteristics of natural forests, and the establishment of a network as the initial step towards a more successful management of forest biodiversity. Remnants of ancient forest may constitute the focal areas, together with newly established forest patches, around which to concentrate management. Newly established forest patches do not have to be very large (Honnay et al. 2002) but it is necessary to spread them geographically in order to establish an archipelago of patches of different size, shape and level of isolation, creating or restoring ecological corridors as well. A recently published plant species check-list of the Venetian district (Masin et al. 2009) has detected the presence of some ancient forest species (*Anemone* sp.pl., *Allium ursinum* L., *Carex remota* L., *Circaea lutetiana* L., *Iris graminea* L., *Polygonatum multiflorum*, etc.) outside the forests, along the oldest hedgerows or inside the old large gardens of Venetian mansion-houses so confirming the important role of spread hedgerows and other connecting elements.

Particularly for older and smaller remnants, new forest parcels should be situated at a minimal distance from the ancient forests, and, if possible, adjacent to them, thus allowing an increase of the existing forest area, and, at the same time, a decrease of the ratio edge area/core area.

If so, the network of patches could potentially function as a metapopulation (Hanski & Gilpin 1997) system where temporary extinction in some patches is compensated by colonization from others. However, in order to achieve this, it is necessary to expand the planning view from the individual woodlots to include the spatial aspects at a landscape level. Especially in the current global change context, therefore, conservation efforts should incorporate the establishment of forest corridors providing species to change their geographical distribution.

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