

Floristic and life form diversity in post-pasture successions on a Mediterranean island (Corsica)

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Abstract

The landscapes of the French island of Corsica are the result of the grazing tradition which has always occupied a pivotal position in the island's economy. Furthermore, in the last fifty years, a reduction in the pressure from human activity has lead to changes in plant cover. This article intends to study the evolution of dynamic mechanisms during the secondary successions and the effect of changes in vegetation on plant diversity. Our study was based on a simultaneous study of 375 plots carried out between May and September from 1996 to 1998. We studied the floristic composition of each stage both qualitatively (life form, adaptive strategy and seed dispersal mode) and quantitatively (species richness, equitability, Shannon index). The results show a change in species and environmental conditions, with a progressive move from heliophilic grassland and low shrub species with an S or SR strategy, anemochoric and with a high tolerance for soil quality to a final stage of dense forest composed of competitive (C or CS) zoochoric or barochoric phanerophytes. Moreover, the turning point in Corsica in terms of floristic diversity lies between 20 and 55 years after land abandonment. Successions are due to a series of rapid interactions. Thus, when a site is given reserve or protected area status, we need to take into account the fact that it will evolve according to the biological traits of the species. From a research point of view, we need to look at process diversity and the role of each of the species present during the successions.

Introduction

A major issue in ecological research involves the effects of species and groups of species on community level and ecosystem level attributes (Ursic et al. 1997; Wardle et al. 1999). The ecological consequences of land abandonment, that is to say secondary successions, have been studied for several decades in many fields of research, although less so in Corsica (Mediterranean region: Escarré et al. (1983); Farina (1991); Tatoni et al. (1994); Tatoni and Roche (1994) and mountain areas: Muller (1992); Delcros (1993); Tappeiner and Cernusca (1993)). However, this Mediterranean island is one of the most suitable areas for studying secondary successions as a result of the

complexity that derives from a context of grazing, fire and urbanisation.

Over the last 50 years, human activity in the central part of Corsica has greatly diminished (Ravasi-Giordani 1983; Panaïotis et al. 1998; Saïd and Auvergne 2000), which has resulted in a natural recolonisation of sites by species. This change in land use has led to a more or less rapid modification in the plant communities (Barbero and Quezel 1988), both qualitatively and quantitatively (Lepart and Escarré 1983; Tatoni and Roche 1994; Fairbairn 1996).

This progressive natural recolonisation is not only of interest to foresters in terms of land management and development, but also to scientists seeking to improve their understanding of the structure, functioning and dynamics of plant communities during sec-

ondary successions. Furthermore, the European Union classifies a large number of plant communities that are the result of human activity (forest clearings, grazing or fire) within the context of biodiversity conservation. It is therefore of interest to study the functioning and the dynamics of communities after land abandonment.

In this context, we want to (i) show the place of plant communities in secondary successions (ii) quantify the time of transition and the length of each dynamic stage during post-pastoral successions.

For this study, we studied 375 sites distributed in nine valleys of central Corsica and agriculturally abandoned since various dates. This island is interesting for the study of dating problems of secondary successions because it has sites with various abandonment dates since the 1750's and we have methods to measure the date of abandonment of sites (Saïd and Gégout 2000).

Materials and methods

Site and species

The climate of the study area is mountainous-Mediterranean with average annual rainfalls of 1400 mm, average annual temperatures which vary from 7° to 10°C and altitude which varies from 700 to 1800 m.

The study area lies essentially on granite under brown acid soils (Roche and Roux 1976). The traditional agriculture on Corsica is livestock farming with cattle, goats and pigs put out to graze.

The nine valleys' landscape is characterised by vast pastures, forests or abandoned areas without hedgerows. The main species of woodland are *Pinus pinaster*, *Quercus ilex*, *Fagus sylvatica*, *Pinus nigra* subsp. *laricio* var. *corsicana*. The pasture is characterised by thorny or toxic shrubs such as *Anthyllis hermanniae*, *Berberis aetnensis*, *Genista lobelii* var. *lobelioides*, or *Juniperus communis* subsp. *alpina* (Saïd and Gégout 2000). Nomenclature was based on Tutin et al. (1964–1980).

Sampling

The sampling strategy was developed to distribute plots according to the age of the oldest woody specimen (Saïd and Gégout 2000).

A total of 375 plots were made in the summers of 1996 and 1998 within the study area.

These nine valleys in Corsica are interesting for the study of dating problems of secondary successions, because they have sites with various abandonment dates since the 1750's. We supposed that the vegetation on a site is the result of a linear dynamic and successional following the same temporal evolution.

Chronological data

The estimation of abandonment period is different if the oldest ligneous species of the plot is a short-lived species or a long-lived species. Hence, the procedure for estimating the abandonment period of a sample plot has been modelled using two linear regressions. So, on each plot the abandonment date was estimated using woody species following the method of Saïd and Gégout (2000):

I – when the oldest woody specimen is a short-lived species (shrub):

$$d = -5.5 + 1.1a \quad (n = 56; r^2 = 0.72; SE = 4.5 \text{ yr}) \quad (1)$$

where d is the abandonment period of the site estimated with aerial photographs (Tanaka and Nakashizuka 1997) and a is the age of its oldest short-lived specimen

II – when the oldest woody specimen is a long-lived species (tree):

$$d = 0.08 + 0.9a \quad (n = 51; r^2 = 0.83; SE = 4.0 \text{ yr}) \quad (2)$$

where d is the abandonment period of the site estimated with aerial photographs (Tanaka and Nakashizuka 1997) and a is the age of its oldest long-lived specimen

We then grouped the samples according to their age to obtain four dynamic stages (age categories): 0 to 15, 15 to 30, 30 to 60 and over 60 years.

Floristic and ecological data

On each plot, a phytoecological investigation was carried out in order to estimate the structural complexity. This investigation included climatic variables (altitude, exposure, slope, topographical situation), several soil features (pH, texture, structure and stoniness of pedological horizons down to 0.5 m) and an evaluation of the cover of main vegetation layers (herbaceous layers < 0.5 m, low shrubs between 0.5 and 2 m, high shrubs between 2 and 8 m and trees > 8 m).

On each plot and layer, the abundance-dominance of all vascular plant species was recorded with a scale of 7 levels (Braun-Blanquet 1932): absence, rare and cover < 5%, abundant and cover < 5%, 5 < cover < 25%, 25 < cover < 50%, 50 < cover < 75%, 75 < cover < 100%.

The functional characteristics of the species at each stage defined with chronological data were used to interpret the inter-stage dynamic mechanisms. To this purpose we looked at:

- life forms of plants (Raunkiaer 1934; Molinier and Muller 1936)
- seed dispersal type (Molinier and Muller 1936)
- plant strategies of Grime, that is to say stress-tolerant species (S), competitive species (C), ruderal species (R) and all the intermediate stages between these three classes (Grime 1979; Grime et al. 1988; Gloaguen et al. 1994). Species whose functional characteristics were unknown (13% of the total species number) were omitted from analysis.

Diversity indices

We used three indices to interpret the diversity within stages:

1. Species richness or α , is the total number of plant species recorded in the homogeneous plot
2. The equitability index (ranges from 0 to 1).

$$e = \frac{\bar{H}}{\log_2 S}$$

- $\log_2 S = H_{\max}$ = maximum possible value for H
3. Shannon's diversity index (Shannon and Weaver 1949) which takes into account the equitability within species distribution; this index is used as a relative index for comparing different stages.

$$H = - \sum_{i=1}^S p_i \log_2 p_i = \text{Shannon value}$$

S = number of species

$$p_i = \frac{a_i}{\sum_{i=1}^S a_i}$$

a_i = cover of species I, coded from 1 to 6.

Statistical analysis

Floristic data were processed using Factorial Correspondence Analysis (FCA) (Ter Braak 1985), using ADE-4 software (Chessel 1995; Thioulouse et al. 1997a, 1997b). Only the first two axes are shown here. Species abundance, equitability and Shannon diversity were calculated using the EcolTools module of the ADE-4 software (Thioulouse and Chessel 1992; Chessel 1995; Thioulouse et al. 1997a, 1997b).

The effect of the stage on all of the preceding parameters was analysed by Analysis of Variance (ANOVA). Analyses were performed using STATVIEW F-5.0 software. When the treatment effect was significant, pairwise mean comparisons were performed with a Fischer's Least-Square-Difference test to point out significant differences between stages.

Results

Patterns of successions

On the ordination diagram of the surveys for the first two axes of FCA, we labelled the different kinds of vegetation stands (Figure 1a) and strongest contributing species (Figure 1b).

The comparison of the two diagrams allows us to find the underlying ecological meaning of these factorial axes quite easily. That is opposing the grassland, low scrub and high scrub against open forest and dense forest. Species characterising (Figure 1b) the negative extremity of the first axis are essentially fallow heliophilic species, with low cover and often resistant to grazing, such as *Genista salzmannii* var. *salzmannii* ou *lobelioides*, *Juniperus communis* subsp. *alpina*, *Thymus herba-barona*. The positive extremity is high cover and sciaphilic species of forest stands (*Fagus sylvatica*, *Fraxinus ornus*). The first axis appears to be a dynamic gradient along which the different stages are grouped regularly, represented by samples that are linked together, especially for the shrub stages. Axis 2 opposes the pole of the mesohydrophilic beech stands with *Luzula pedemontana* to xerophilic pine stands. This axis has a strong correlation with temperature and rainfall. It is therefore a climate axis, which will not be considered further.

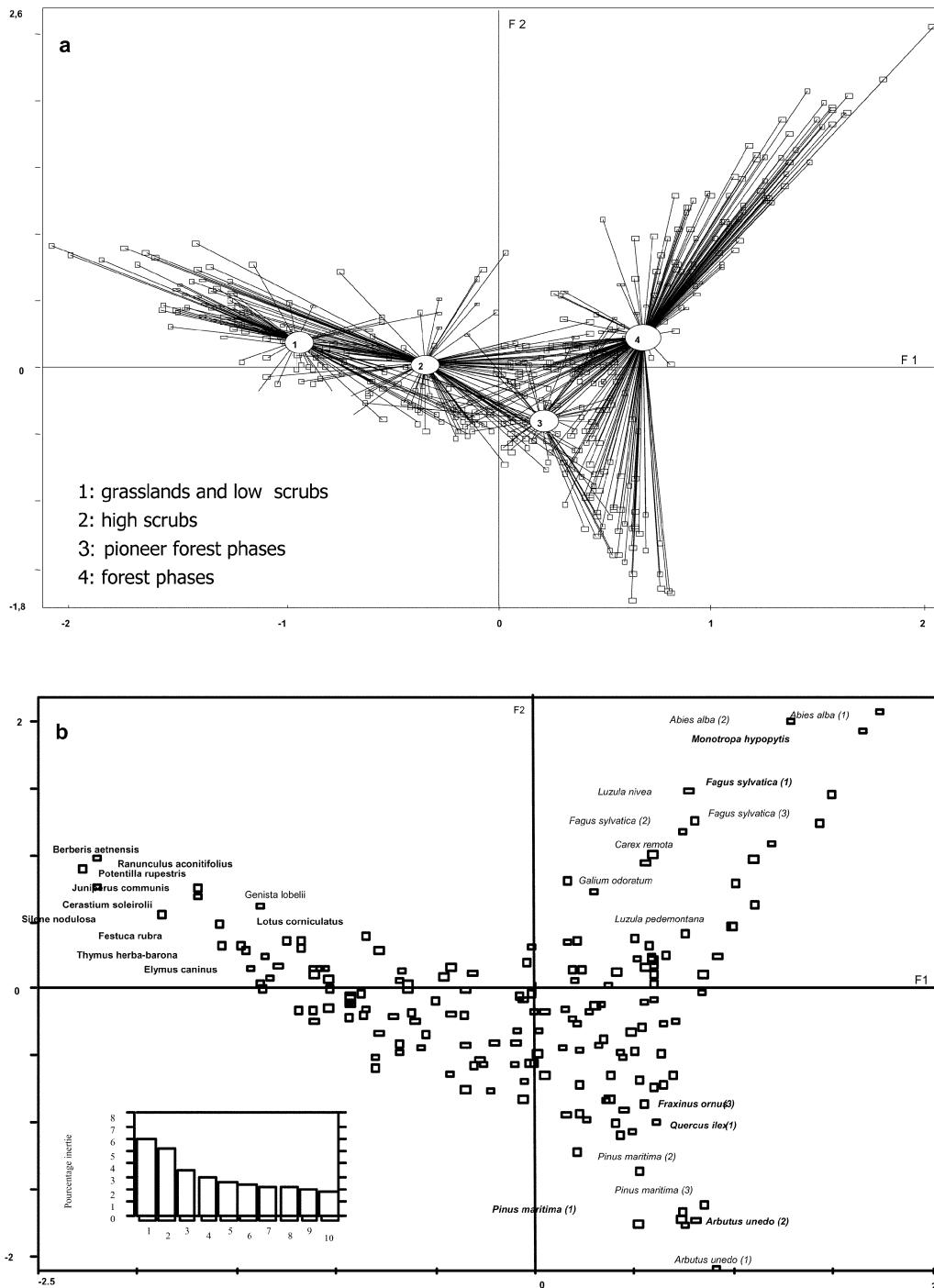


Figure 1. (a) CA on floristic data: ordination for the first two axes; (b) projection of strongest contributing species (the most significant species for axis 1 are in bold, for axis 2 in italics and in bold italics for those that contribute to both axes. The number at the end of the name for woody species separates individuals occurring in tree (1), shrub (2) and seedling (3) layers.

Evolution of abundance and diversity during the secondary successions.

Figures 2a–c show the same curve trajectory for diversity indices during the secondary successions. Furthermore, Shannon's diversity index and the species richness show a significant correlation ($n = 375$; $SE = 0.152$; $r^2 = 0.97$; $p < 0.0001$). Change in species richness and the Shannon's diversity index shows three main stages: increase in grasslands (18.7) and low scrub (20.6), stabilisation in the intermediate stages (high shrub and pioneer forest phases: 20.8) and decrease in dense forest stages (17.2) (Figure 2). On the other hand, equitability during secondary successions does not follow the same trajectory as the other diversity indices; it appears to be stable during the successions with a slight tendency to diminish over time. In fact, using Fischer's LSD test, at a threshold of 5%, we find no significant differences between the transitional stages and the low scrub phase.

The ANOVA carried out on the "stage" factor on the diversity indices demonstrates a correlation between the dynamic stages and these indices ($df = 3$, $F = 3.8$; $p < 0.01$ for species richness and $df = 3$, $F = 2.9$; $p < 0.03$ for Shannon's diversity index).

Evolution of life form system of species during secondary successions

The ANOVA carried out shows a highly significant "stage" effect for all types of biological form except for geophytes (Figure 3a; Table 1a). The hemicryptophyte count decreases quickly after land abandonment, but it dominates during the secondary successions. The hemicryptophytes, therophytes and chameophytes decrease, in favour of the phanerophytes. The continual increase of the phanerophytes results from colonisation by woody plants, which only allow their own regeneration. Contrary to other regions (Kollman, 1997 in mountain areas and Tatoni and Roche (1994) in the Mediterranean region), Corsica has extremely few therophytes in all the stages considered: their proportion does not exceed 7% (whatever the stage) during secondary successions.

Evolution of the dissemination mode of species during secondary successions

There is a highly significant "stage" effect on the type of seed dispersal, whichever dispersal mode we look

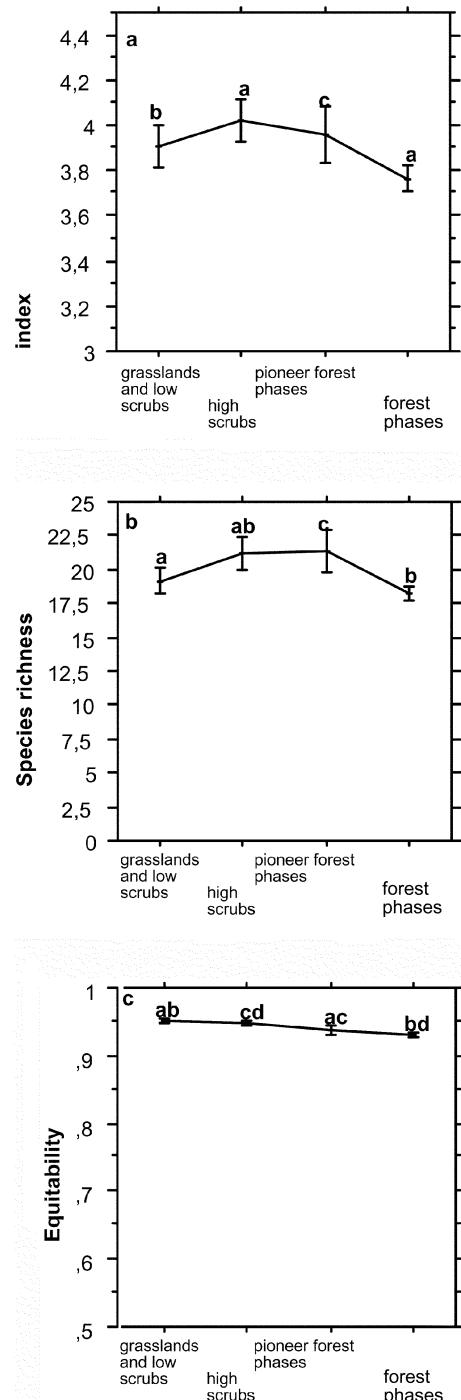


Figure 2. Evolution of diversity (abundance (a), Shannon's diversity index (b) and equitability (c)) during secondary succession. Data represent means and bars indicate standard deviations. When stage effect was significant, a pairwise mean comparison between stages has been performed using a Fisher LSD test (letters denote significant differences at $p = 0.005$)

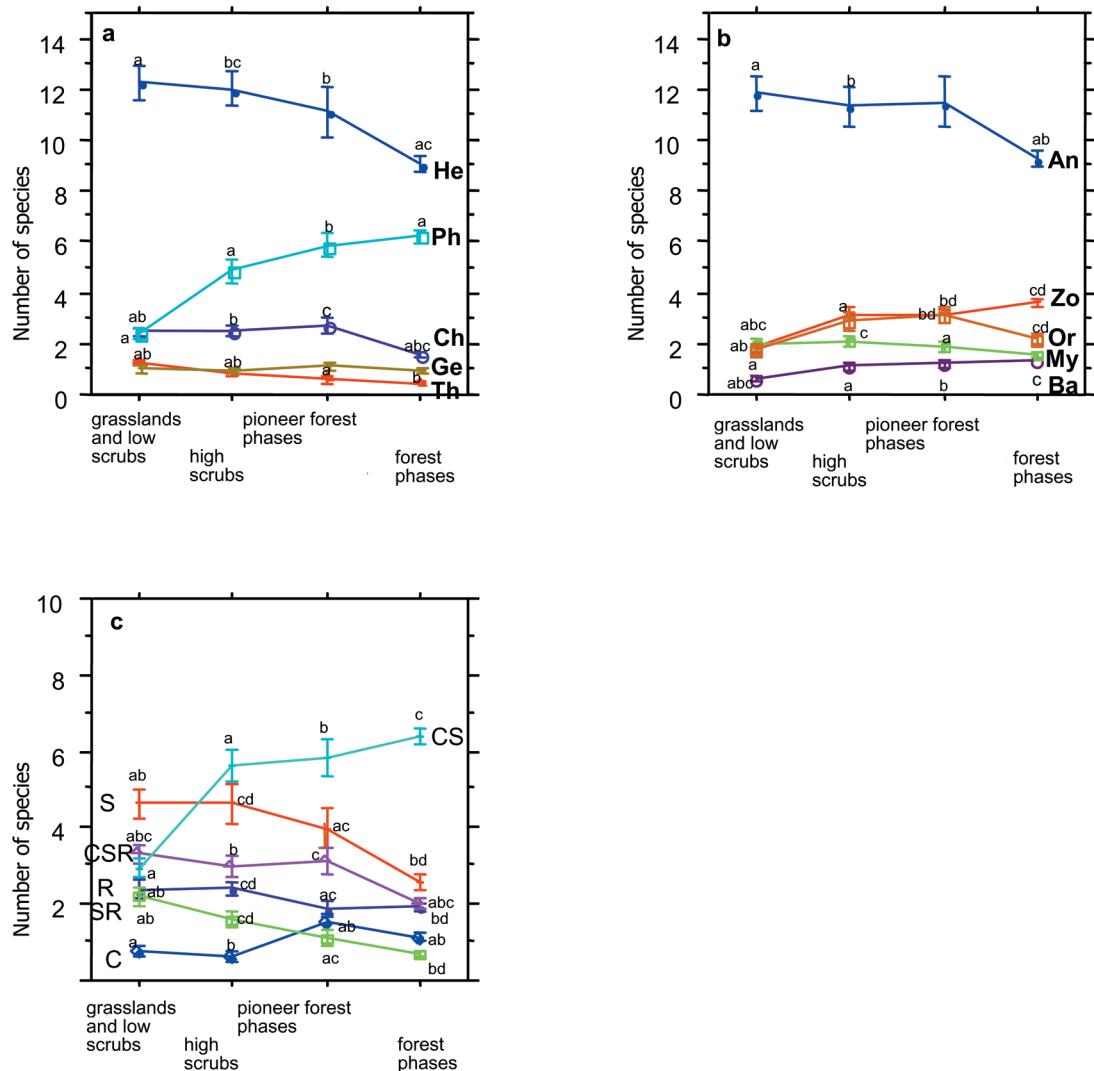


Figure 3. Evolution of the frequency of life-form (a), dissemination modes (b) and adaptive strategies (c) of species during secondary succession. Data represent means and bars indicate standard deviations. Results of ANOVA are mentioned in Table 1. When stage effect was significant, a pairwise mean comparison between stages has been performed using a Fisher LSD test (letters denote significant differences at $p = 0.005$).

Ch: Chamophytes, Ge: Geophytes, He: Hemicryptophytes, Ph: Phanerophytes, Th: Therophytes, An: Anemochory, Ba: Barochory, My: Myrmecochory, Or: Ornithochory, Zo: Epi or Endozoochory.

at. The anemochoric species, generally annuals, are the first to colonise after land abandonment. Subsequently, re-afforestation entails a change in the vertical structure and a modification of the microclimate, where vegetation changes to favour epi- or endozoochoric and barochoric species (Figure 3b; Table 1b) (Debussche et al. 1996). We observe an important dispersal role for birds and ants in the intermediate stages of the successions (essentially high shrub). Thus the invasion of trees and shrubs of ornithochoric

dissemination type is apparent in the middle of the successions.

Adaptive strategies adopted by species during secondary successions

A substantial ($p < 0.0001$) “stage” effect can also be observed for all of the types we studied, with the exception of the type R species which were less significantly influenced by the evolutionary stage, and the

Table 1. Results of the ANOVA (+/- SE) between the dynamic stage and the Grime adaptive strategies, the dissemination mode and the life form of the species during the secondary succession.

a) plant strategies	df	F-ratio	p
C	3	6.4	***
error	371		
S	3	13.4	***
error	371		
R	3	5.3	**
error	371		
CSR	3	9.8	***
error	371		
CR	3	1.4	ns
error	371		
CS	3	23.3	***
error	371		
SR	3	19.9	***
error	371		
b) Seed dispersal type	df	F-ratio	p
Epi-endozoochory	3	14	***
error	371		
Myrmécochorie	3	2.9	*
error	371		
Anemochory	3	5.7	**
error	371		
Ornithochory	3	4.2	**
error	371		
Barochory	3	11.3	***
error	371		
c) Life-form	df	F-ratio	p
Champhytes	3	10.7	***
error	371		
Geophytes	3	0.4	ns
error	371		
Hemicryptophytes	3	10.6	***
error	371		
Therophytes	3	16.6	***
error	371		
Phanerophytes	3	26.5	***
error	371		

Significance level according to one way ANOVA is indicated as follows †: ns = non significant, *p = 0.05; **p = 0.005, ***p = 0.0001.

CR species that were not influenced by the evolutionary stage. We can observe an evolution in species' adaptive strategies during the evolutionary stages (Figure 3c; Table 1c).

These results would indicate the progressive installation of species (SR and S) capable of optimal

growth in undisturbed or weakly stressed conditions, whereas species from disturbed environments become less competitive (CS and C) in secondary successions (Figure 3c; Table 1c). Between these two extremes, we can observe a gradient.

Discussion

Differentiation of evolutionary stages

Using the chronological variable in secondary successions also allows us to link the floristic composition of each stage to an abandonment date. This evolution in the vegetation is very rapid and it requires on average less than half a century to pass from a grassland stage to a forest stage with much more rapid dynamics in the first succession stage. In Corsica, high shrub appears a maximum of 15 years after the installation of low scrub and, thirty years later, is replaced by forest. The significance of classification of stage is the fact that we take into account the abandonment date and also the changes in flora. We can therefore establish that it takes less than 60 years after the end of grazing before forest vegetation can be observed and beyond that date the vegetation hardly changes.

Floristic diversity

The abandonment of grazing leads to an increase then a decrease in species diversity in plants during secondary successions (Figure 2). The lower number of species in the evolved forest phases is due to the disappearance of annual species, which have a strong presence in scrubs. They are not compensated by the appearance of herbaceous forest species, where we observe a low level of herbaceous cover and the lowest equitability index, even if the variations are small. On the other hand, the low diversity in the low scrub stages is a result of grazing that is not intense but nevertheless present at these stages (Figure 3). Our results confirm the studies on vegetation in the Mediterranean region (Tatoni and Roche 1994; Debussche et al. 1996; Le Floc'h et al. 1998) and in mountain areas (Muller 1992) which observe an irregular evolution of biodiversity during successions, culminating in the intermediate stages (Whittaker 1969; Whitmore 1982; Alard et al. 1998). On the other hand, Bazzaz (1975) found a continuous increase in plant diversity during successive stages of colonisation of fallow

land in Illinois. In fact, it seems that the most advanced stage studied by Bazzaz (1975) is not more than 40 years old (Danaïs 1982), this optimum coinciding with the intermediate stages, between 20 and 55 years after land abandonment. In this stage we observe heliophilic species but also the beginning of the installation of sciaphilic and semi-shade species and we find the maximum of heterogeneity and habitat diversity (Figure 3). These results support the conclusions of Delcros (1999), who states that it is necessary to wait 20 years to obtain optimum floristic diversity.

What are mechanisms?

The results show the successional patterns of abandoned land with a change in species once disturbance has ended. We find a closing-off of abandoned land with a change in interstage diversity and also in the composition of the plant communities (Table 1) (Bews 1917; Tatoni and Roche 1994; Debussche et al. 1996). A reduction in grazing pressure has allowed the installation of species which are anemochoric (Figure 3b), heliophilic and undemanding in terms of soil quality, that is to say herbaceous SR species (*Lotus corniculatus*, *Teucrium marum*) (Grime 1979) or stress tolerant species (*Aira caryophyllea*, *Nardus stricta*, *Petrorhagia saxifraga*) (Grime 1979) and less competitive species (Pickett 1980; Tilman 1990; Tilman and Pacala 1993). These species are often present in pastures before abandonment, but in a dormant state (Oosting and Humphreys 1940; Lepart and Escarré 1983). The presence of livestock in pasture favours the selection of thorny (*Genista lobelii* var. *lobeloides*, *Juniperus communis* subsp. *alpina*), scented (*Helichrysum italicum* subsp. *italicum*) or toxic (*Helleborus lividus* subsp. *corsicus*) (Gamisans 1999) species in the shrub. Subsequently, the grassland and shrub species, often opportunistic (r-strategists) (Odum 1969; Newell and Tramer 1978; Barbault 1997) and incapable of invading or increasing in the presence of other species diminish. It appears that in Corsica the constant presence of thorny pioneer species in the early stages of the successions can be explained by the way one plant improves the survival and growth potential of another (Callaway 1992, 1995, 1997; Saïd and Gégout 2000). Moreover, the woody specimens will form a vertical structure that will serve as perches for birds. Thus the accumulation of excreta and regurgitated matter under the tree will facilitate the installation of many ornithochoric

species in this stage (Debussche et al. 1982). Myrmecochoric distribution seems to be due to the facilitation of these species by ants after burning has been carried out in the grassland and low scrub stages, the seeds accumulated in the anthill before the fire being capable of rapid germination after the vegetation has been destroyed (Lepart and Escarré 1983). These species will be replaced by barochoric and more competitive species (*Abies alba*, *Fraxinus ornus*) (Callaway 1992, 1995, 1997; Callaway and Walker 1997), but also CS and zoochoric species (*Fagus sylvatica*, *Quercus pubescens*, *Rubia peregrina*, *Quercus ilex*) (Lepart and Escarré 1983; Debussche et al. 1996). These species often have significant reserves that allow them to face up to environmental constraints and to competition with other species but do not favour rapid installation (Lepart and Escarré 1983; Debussche et al. 1996). In contrast to other authors (Escarré et al. 1983; Lepart and Escarré 1983), we observed a significant number of anemochoric species even in the forest stages (more than 40% of the total number of species in this stage), as the majority of forests at altitude are pine stands of Corsican or maritime pine. These trees are themselves anemochoric and do not form significant cover, which in turn allows the installation of heliophilic species among which there are many anemochoric species.

Implications for management and conservation biology

For biodiversity conservation, the importance of our research has been to be able to quantify the length of each secondary succession stage in order to understand better the duration of the pivotal period during which maximum levels of diversity and species richness are reached. Data shows the transition period (shrub stages) of species and a change in species' adaptive strategy to environmental conditions, inter-species competition and dissemination.

From a research point of view, we need to look at the diversity in processes and the role that each of the species present in the successions adopts. In fact, it is important to protect all of the processes linked to structural species even if some of them seem commonplace in themselves. This objective would be hard to achieve if land management were discontinued, but an improved understanding of the species forming each of the plant communities is also necessary. It is necessary to study the communities individually, but also within their communities and to con-

sider the landscape in its entirety, not just its constituent elements. Thus if a site is accorded reserve or protected area status, we should take into account the fact that it will undergo rapid evolution due to the biological traits of the species.

The interest of our research methods, with regards to those aims, therefore lies in our use of a chronological variable that allows us to work within a range from a decade up to a century and which compensates for the problem of temporality.

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References

- Alard D., Poudevigne I., Dutoit Th. and Decaens Th. 1998. Dynamique de la biodiversité dans un espace en mutation. Le cas des pelouses calcicoles de la basse vallée de la Seine. *Acta Oecologica* 19: 275–284.
- Barbault R. 1997. Biodiversité, Les Fondamentaux. Hachette, Paris, 159 p.
- Barbero M. and Quezel P. 1988. L'Évolution du couvert forestier dans la région Provence-Alpes-Côte d'Azur en relation avec la déprise rurale. Biogéographie Environnement, Aménagement, CNRS-Éd, Paris, pp. 199–212.
- Bazzaz F. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56: 485–488.
- Bews J.W. 1917. The plant succession in the Thornveld. *S. Afr. J. Sci.* 14: 150–160.
- Braun-Blanquet J. 1932. Plant Sociology, The Study of Plant Communities. McGraw-Hill Book Company, New-York.
- Callaway R.M. 1992. Effect of shrubs on recruitments of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73: 2118–2128.
- Callaway R.M. 1995. Positive interactions among plants. *The Biological Review* 61: 306–349.
- Callaway R.M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112: 143–149.
- Callaway R.M. and Walker L.R. 1997. Competition and facilitation: synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.
- Chessel D. Université Lyon I 1995. ADE-4. Ordination Sous Contraintes. Institut d'Analyse des Systèmes Biologiques et Socio-Economiques, Lyon.
- Collins S., Glenn S. and Roberts D.W. 1993. The hierarchical continuum concept. *Journal of Vegetation Science* 4: 149–156.
- Daget P. and Godron M. 1982. Analyse fréquentielle de l'écologie des espèces dans les communautés. Masson, Paris, 163 p.
- Danais M. 1982. La diversité en écologie: analyse bibliographique. *Botanica rhedonica*, A 17: 77–104.
- Debussche M., Escarré J. and Lepart J. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. *Vegetatio* 48: 255–266.
- Debussche M., Escarré J., Lepart J., Houssard C. and Lavorel S. 1996. Changes in mediterranean plant succession: old-fields revisited. *Journal Vegetation of Science* 7: 519–526.
- Delcros P. 1993. Ecologie du paysage et dynamique post-culturelle en zone de montagne, Grenoble I. Université Joseph Fourier/CEMAGREF, Grenoble.
- Delcros P. 1999. Fermeture des paysages et modifications de la biodiversité: Etat des Connaissances et perspectives. CEMAGREF, Grenoble, Musée National d'Histoire Naturelle 100 p.
- Escarré J., Houssard C., Debussche M. and Lepart J. 1983. Evolution de la végétation et du sol après abandon cultural en région méditerranéenne: Étude de succession dans les garrigues de MontPELLIÉRAIS (France). *Acta Oecologia, Oecologia Plantarum* 4: 221–239.
- Fairbairn J. 1996. The forest transition in France. Department of geography, University of Aberdeen, 45 p.
- Farina A. 1991. Recent changes of the mosaic patterns in a mountain landscape (north Italy) and consequences on vertebrate fauna. Option méditerranéennes, série A 15: 121–134.
- Flores-Martinez A., Ezcurra E. and Sanchez-Colon S. 1994. Journal of Ecology, Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology* 82: 325–330.
- Gamisans J. 1999. La végétation de la Corse. Edisud.
- Glatzel G. 1991. Internal proton generation in forest ecosystems as influenced by historic land use and modern forestry. *Fertilizer Research* 27: 1–8.
- Gloaguen J.C., Rozé F., Touffet J., Clément B. and Forgeard F. 1994. Etude des succession après abandon des pratiques culturales en Bretagne. *Acta botanica Gallica* 141: 691–706.
- Grime J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley & sons, Sheffield, 222 p.
- Grime J.P., Hodgson J.G. and Hunt R. 1988. Comparative Plant Ecology. Unwin Hyman, London, 742 p.
- Le Floc'h E., Aronson J., Dhillon S., Guillerm J.L., Grossmann A. and Cunge E. 1998. Biodiversity and ecosystem trajectories: first results from a new LTER in Southern France. *Acta Oecologica* 16: 285–293.
- Lepart J. and Escarré J. 1983. La succession végétale, mécanismes et modèles: analyse bibliographique. *Bulletin d'Ecologie* 14: 133–178.
- Molinier R. and Muller P. 1936. La dissémination des espèces végétales. *Revue générale de botanique*. 594-597, pp. 53-72, pp. 152-169, pp. 202-221, pp. 277-293, pp. 341-358, pp. 397-414, pp. 472-488, pp. 533-546, pp. 598-614, pp. 649-670.

- Muller S. 1992. Analyse synchronique des successions végétales après déprise agricole dans les vallées des Vosges du Nord. Annales scientifiques de la Réserve de la Biosphère des Vosges du Nord 2: 53–67.
- Newell S.J. and Tramer E.J. 1978. Reproductive strategies in herbaceous plant communities during succession. Ecology 59: 228–234.
- Odum E.P. 1969. The strategy of ecosystem development. Science 164: 262–270.
- Oosting H.T. and Humphreys M.E. 1940. Buried viable seeds in a successional series of old field and forest soils. Bulletin of torrey botanical club 67: 253–273.
- Panaïotis C., Loisel R. and Roux M. 1998. Analyse de la réponse de la végétation aux trouées naturelles dans une futaie, gérée de *Quercus ilex* L. en Corse (île Méditerranéenne). Canadian Journal of Forest Research 28: 1125–1134.
- Pickett S.T.A. 1980. Non-equilibrium coexistence of plants. Bull. Torrey Bot. Club 107: 238–248.
- The life-forms of plants and plant geography. Raunkiaer C. 1934..
- Ravis-Giordani G. 1983. Bergers Corses. Les communautés villa-geoises du Niolu. Edisud.
- Roche D. and Roux C. 1976. Les sols d'une séquence bioclimati-que méditerranéo-montagnarde en Corse cristalline, mémoire de D.E.A. C.E.P.E. Montpellier - I.N.A., Paris, 87 p.
- Saïd S. and Auvergne S. 2000. Impact du pastoralisme sur l'évolution paysagère en Corse: quelques propositions de ges-tion. Revue de Géographie Alpine 3: 39–49.
- Saïd S. and Gégoût J-C. 2000. Using the age of the oldest woody specimen for post-pasture successions in Corsica (Mediterranean island). Acta Oecologica 21: 193–201.
- Shannon C. and Weaver W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.
- Tanaka H. and Nakashizuka T. 1997. Fifteen years of canopy dy-namics analysed by aerial photographs in a temperature deciduous forest, Japan. Ecology 78: 612–620.
- Tappeiner U. and Cernusca A. 1993. Alpine meadows and pastures after abandonment. Pirineos 141-142: 97–115.
- Tatoni T., Magnin F., Bonin G. and Vaudour J. 1994. Secondary successions on abandoned cultivation terraces in calcareous Provence. I- Vegetation and soil. Acta Oecologica 15: 431–447.
- Tatoni T. and Roche P. 1994. Comparison of old-field and forest revegetation dynamics in Provence. Journal of Vegetation Sci-ence 5: 295–302.
- Ter Braak C.J.F. 1985. Correspondence analysis of Incidence and Abundance Data: Properties in Terms of a Unimodal Response Model. Biometrics 41: 859–873.
- Thioulouse J. and Chessel D. 1992. A method for reciprocal scal-ing of species tolerance and sample diversity. Ecology 73: 670–680.
- Thioulouse J., Chessel D., Dolédec S. and Olivier J.M. 1997a. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing 7: 75–83.
- Thioulouse J., Chessel D., Dodélec S. and Olivier J.M. 1997b. ADE-4: Stacks and Program library for the analysis of envi-ronmental data. Elsevier, Amsterdam.
- Tilman D. 1990. Constraints and tradeoffs: toward a predictive the-ory of competition and succession. Oikos 58: 3–15.
- Tilman D. and Pacala S. 1993. The maintenance of species rich-ness in plant communities. In: Ricklefs R.E. and Schlüter D. (eds), Species diversity in ecological communities. University of Chicago Press, Chicago, pp. 13–25.
- Tutin T.G., Heywood V.H., Burges N.A., Moore D.M., Walters S.M. and Webb D.A. 1964–1980. Flora Europaea. Vol. 5. Cam-bridge University Press, Cambridge.
- Ursic K.A., Kenkel N.C. and Larson D.W. 1997. Revegetation dy-namics of cliff faces in abandoned limestone quarries. J. Appl. Ecol. 34: 289–303.
- Wardle D.A., Bonner K.I., Barker G.M., Yeates G.W., Nicholson K.S., Bardgett R.D. et al. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil diversity, and ecosystem properties. Ecological Monographs 69: 535–568.
- Whitmore T.C. 1982. On pattern and process in forests, in the plant community as a working mechanism. In: Newman E.I. (ed.), The plant community as a working mechanism. Blackwell, Ox-ford, pp. 45–49.
- Whittaker R.H. 1969. Evolution of diversity in plant communities, Brook. Symp. on Biol. 22: 178–196.