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Effects of soil surface disturbances after logging on plant functional types

Hélène GONDARD^{a*}, Marc DECONCHAT^b

^a Centre National de la Recherche Scientifique, Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, 1919 route de Mende, 34293 Montpellier Cedex 5, France

^b Institut National de la Recherche Agronomique, BP 27, 31326 Castanet-Tolosan, France

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Abstract – Soil surface disturbances after logging influence plant species diversity. To estimate these effects, the objective of the present study was to test three hypotheses: (1) each soil surface disturbance type is characterized by a group of plant species that emerges following the disturbance, (2) each emergent group of plant species has distinct, recognizable biological traits, (3) in two different bio-geographic plant communities, each soil surface disturbance type is characterized by the same set of biological traits. We present results from Atlantic oak (*Quercus pubescens* Willd., *Q. robur* L. and *Q. petraea* (Mattuschka) Liebl.) coppices and natural Mediterranean Aleppo pine (*Pinus halepensis* Miller) forests of southern France. Both studies use the same methodology based on a typology of soil surface perturbation 1–3 years after logging combined with a vegetation inventory. Plant functional traits (morphological, life history and regeneration), not necessarily linked with taxonomic attribution, were used to constitute putative functional groups to allow comparison between the two studies. Results were similar in the two studies and confirmed the working hypotheses.

plant species / logging / soil surface disturbance / life traits

Résumé – Effets des perturbations de la surface du sol dues à l'exploitation forestière sur la diversité végétale. Les perturbations de la surface du sol dues à l'exploitation forestière sont susceptibles d'agir sur la diversité végétale. Pour estimer ses effets, l'objectif était de tester trois hypothèses : (1) chaque type de perturbation de la surface du sol est caractérisé par un groupe d'espèces qui se présente après la perturbation, (2) ces groupes d'espèces ont des traits biologiques distincts, (3) dans deux communautés bio-géographiques différentes, chaque type de perturbation de la surface du sol est caractérisé par les mêmes traits biologiques. Nous présentons les résultats obtenus dans le cas de taillis de chênes (*Quercus pubescens* Willd., *Q. robur* L. and *Q. petraea* (Mattuschka) Liebl.) de la région atlantique et des forêts de pin d'Alep (*Pinus halepensis* Miller) de la région méditerranéenne du sud de la France. La méthodologie, utilisée dans les deux études, est basée sur une typologie des perturbations de la surface du sol dans les trois premières années qui suivent l'exploitation forestière combinée avec des relevés de végétation. Des traits fonctionnels (traits morphologiques, d'histoire de vie et de régénération), sans attribution taxonomique particulière, ont été utilisés pour permettre une comparaison entre les deux études. Les résultats étaient similaires dans les deux études et confirment les hypothèses.

diversité végétale / exploitation forestière / perturbation de la surface du sol / traits de vie

1. INTRODUCTION

In recent years, there has been much concern about the impact of forest management practices on biodiversity [8, 19, 52]. Society increasingly demands that forest managers reduce the negative influences of their exploitation practices on biodiversity, especially during logging operations that are the most obvious human perturbations on forests. Consequently, considerable research has been carried out on this topic, especially concerning plant species diversity which is a component of prime importance in terrestrial ecosystem functioning [2, 7, 34].

Plant species diversity in managed temperate forests is generally strongly modified just after logging perturbations, with

an increase of species richness [26, 31]. When the canopy closes, species richness decreases and can return to its former level [32]. However, even if species richness decreases, rare species can develop in old forests and thus yield enhanced conservation value [11, 61]. Logging changes canopy structure and induces large understorey modifications with regards to light [21, 67], rainfall distribution on soil [1, 10], temperature and humidity [9], as well as chemical and microbiological soil properties [18, 37, 44, 51]. All these factors have effects on species diversity and thus on resistance [43], resilience [58] and overall functioning of ecosystems. The modifications of the ground surface, such as slash deposition and litter removal, created by logging operations, are suspected to be possible driving factors of plant species diversity. These perturbations

* Corresponding author: gondard@cefe.cnrs-mop.fr

of the ground surface create a heterogeneity that could have consequences on plant species diversity [15, 27, 56].

To analyze ecosystem responses to disturbances, life traits appear to be an excellent tool [31, 42]. Indeed, plant functional types can be defined as comprising species that respond in a similar fashion to specific environmental factors, as a result of their shared biological traits [40]. Functional classifications, based on life traits, give biological robustness and cross-regional comparability to models and field studies [38]. Life traits are morphological, physiological or ecological traits, not necessarily linked with taxonomic attribution [50]. Thus, plant functional classification has recently received much attention from ecologists even though functional classifications of species are known and used since quite some time [66]. The use of life traits for the comprehension and analysis of plant species dynamics in relation with perturbation is clearly demonstrated by many authors [16, 17, 41, 45, 47]. These authors generally concur with a general hypothesis that there exists a pattern of response to perturbation, linked to species biology, which is more or less identical for plant communities belonging to vastly different milieux and contexts [46].

The objective of the present paper is to use functional groups based on plant life traits in order to analyze effects of soil surface disturbances after commercial logging on plant species diversity. For that purpose, we test three hypotheses: (1) each soil surface disturbance type is characterized by a group of plant species, (2) each emergent group of plant species has distinct, recognizable biological traits, (3) in two different bio-geographic plant communities, each soil surface disturbance type is characterized by the same set of biological traits. These hypotheses have been tested by combining two separate studies employing similar methodologies in two types of forests.

2. MATERIALS AND METHODS

The two types of forests studied are located in southern France. The first one, hereafter called Atlantic (ATL), is near Toulouse in a region with Atlantic climatic influence (800 mm mean annual precipitation; 11 °C mean annual temperature; 200–400 meters above sea level; molasses substratum). Broad-leaved trees including oaks (*Quercus pubescens* Willd., *Q. robur* L. and *Q. petraea* (Mattuschka) Liebl.), chestnut (*Castanea sativa* Miller) and cherry (*Prunus avium* L.) are the main canopy species of the highly fragmented forests which are generally managed in coppice, and coppice with standards, since several centuries. There are few recent afforestations in the area and most of the woodlots were already present before the beginning of the twentieth century judging by old maps. This area has been studied in 1998 [13].

The second area studied in 1999 [25], hereafter called Mediterranean (MED), is near Draguignan, in southeastern France, in a region with Mediterranean climatic conditions (800 mm mean annual precipitation; 14 °C mean annual temperature; 200–300 m a.s.l; limestone substrate) [39]. The studied forests are composed of Aleppo pine (*Pinus halpensis* Miller) stands, with evergreen holm oak (*Quercus ilex* L.) and downy oak (*Quercus pubescens* Willd.) in the under canopy. Since the nineteenth century, abandonment of olive trees and vineyards culture, the decline of grazing, and the spread of plant diseases have favoured the expansion of Aleppo pine to the detriment of holm oak [3, 60]. This pine is a transient species which, being unable to reproduce in its own understorey, is replaced by holm

oak or downy oak in the absence of fire. Logs of these Aleppo pine-dominated forests are mainly harvested for transformation in regional paper pulp factories.

In these forests, the description of the ground surface, in stands logged since less than three years, was inspired from the method developed by McMahon [48]. This method is based on visual recognition of the ground surface at selected points or spots (30 cm radius circle) with regard to a reference list of 23 possibilities. As many ground surface classes had low frequencies in our studies, we simplified the classes of the original reference list into three broad groups: N = not perturbed, P = perturbed (litter removed but topsoil intact, litter and topsoil mixed, rut etc.), R = remnant depot (slash cover deep) [14]. Data collection on plant species composition was carried out on the same spots as the ground surface description in the MED area and on a 1 square meter in ATL.

In ATL, the sample was based on two sites with 3 and 4 plots, respectively, and for each one a transect of 20 spots ($n = 140$) was set up. The transects were perpendicular to the main axis of wood transportation on the stand. In MED, the sample was based on 3 sites with five 400 m² circular plots in each, made up by 100 spots along 3 regularly spaced diameters ($n = 1500$). These data were synthesized in order to obtain a measure of the affinity of the observed plant species for each type of ground surface. Assuming Ni, Ri, Pi were the number of presence of the species i in each respective ground surface type and N, R, P the total number of samples of each type, the affinity for type N was calculated as: $FNi = (Ni/N)/(Ni/N + Ri/R + Pi/P)$, and similarly for R and P. When a species was observed only in the N type, $FNi = 1$. When it was never observed, $FNi = 0$. For a given species i, FNi , FRi and FPi defined coordinates in a triangular system where each species was plotted for each studied area. We defined 7 groups of species called N, R, P, NP, NR, PR, NRP. The species of the group N had a specificity $FNi \geq 0.75$, idem for R and P, a species of the group NP had a specificity $FRi \leq 0.25$ and $FPi \geq 0.25$ and $FNi \geq 0.25$, idem for NR and PR, the remaining species are in the group NRP.

To analyze the influence of ground surface modification on plant species diversity after logging, species were characterized by life traits that refer to structure and functioning [40]. We selected here the life forms, defined by Raunkjær [63], which are based on the position on the plant of renewal buds from which new organs and foliage develop after an unfavorable season, such as a cold winter. Life forms (or growth forms) give relevant and revealing information of functional ecological shifts taking place at the community or ecosystem levels [35, 55]. Moreover, life forms effectively synthesize various life history traits, as they integrate both morphological and physiological attributes [22, 23]. The life forms selected in our study are: therophytes (annual plants), geophytes (bulbous plants), hemicryptophytes (herbaceous perennials), chamaephytes (shrubs) and phanerophytes (trees).

Dynamic ecosystem patterns and processes can also be studied by dispersal modes that are important for plant species survey and community structure [5]. Among the different classifications of species based on seed dispersal vectors [65], we selected, after examining the available data, four main dispersal modes: anemochory (seeds dispersed by wind), endozoochory (dispersal associated with ingestion of seeds by animals), epizoochory (seeds dispersed by animals without being ingested) and other dispersal vectors (seeds dispersed by water, gravity and unknown dispersal modes). We also analyzed plant species distribution as a function of their capacity to grow in a restricted area, like a logging area, by using Grime's classification system [29] which allows classifying plant species in relation to their sensitivity to stress tolerance (S), competitiveness (C) and ruderality (R). Competitive strategy "involves selection for highly competitive ability, which depends upon plant characteristics that maximize vegetative growth in productive, relatively undisturbed conditions" [29]. By contrast, stress tolerant strategy is associated with "reductions in both vegetative and reproductive vigor, adaptations which allow

endurance of continuously unproductive conditions arising from environmental stress, severe resource depletion by the vegetation, or the combined effect of the two" [29]. Ruderal strategy "is associated with a short life span and with high seed production and has evolved in severely disturbed but potentially productive environments" [29]. The mean positions of the species groups in the triangle defined by Grime between *R*, *S* and *C* components defined the overall strategies of the groups.

Information about these various traits was obtained for the ATL site from Rameau et al. [62] for life forms and dispersal modes, and from Grime et al. [30] for Grime strategies. In the MED site, we used the data base BASECO (IMEP, Marseille, France) for all life traits [24]. This data base gives information about life traits of Mediterranean plant species from literature [6, 12, 36, 49, 57, 62, 65].

For each group of species defined by affinity for ground surface types, we computed the proportion of species belonging to the classes defined by a given life trait. These proportions were tested against a random distribution of the species by the Pearson χ^2 test with Systat 9 when the number of species was higher than the required number of five; otherwise groups were merged [64].

3. RESULTS

In both study areas; plant species composition differed according to ground surface condition (Fig. 1). In both areas, of the 79 species observed in ATL and the 71 species observed in MED, only 3 species and 5 species, respectively, were exclusively associated with intact spots (i.e., not logged). Conversely, most of the species were observed in intact spots; 43 (9 NP and 34 NRP) in ATL, and 42 (7 NR, 3 NP and 32 NRP) in MED. Perturbation of the ground surface seems necessary for many species that were observed only in such situations – 29 (37% of total species richness) in ATL, and 13 (18% of total species richness) in MED. The species associated with slash decomposition were less numerous; 0 in ATL and 4 in MED. It seems that more species have a high frequency in slash depots in MED than in ATL. Only 14 species are common between both samples (Fig. 1), but they did not have similar trends with ground surface types, except for *Cytisus scoparius*, *Hedera helix*, *Ligustrum vulgare* and *Rubia peregrina* associated with NRP, while *Lolium perenne* and *Teucrium chamaedrys* associated with P in the both areas.

3.1. Raunkiaer's life forms

Geophytes, therophytes and chamaephytes were the life forms least often observed in the two areas (Fig. 2). Only one geophyte, *Tamus communis*, was observed in ATL - NR, and no geophyte at all was recorded in MED. We found only 8 therophytes in ATL of which 1 in N, 5 in P and 2 in NP, and only 4 therophytes in MED of which 1 in R, 2 in P, 1 in NP; most of the therophytes appeared in perturbed places. Chamaephytes represented only 7.1% of the total species richness in ATL and 11.3% in MED; they were observed in several ground surface types but with few species. Hemicryptophytes and phanerophytes were the most observed life forms in the two regions. Hemicryptophytes represented 52.5% of total species richness in ATL and 31.3% in MED, while phanerophytes represented 31.3% of total species richness in ATL and 52.1% in MED. Thus, the statistical analyses were carried out only with these life forms. In ATL, we recorded signifi-

cantly more hemicryptophytes than phanerophytes in perturbed places (P, PR, NP, NPR; $\chi^2_{(2)} = 22.87$; $p < 0.001$), whereas no significant difference were found in MED ($\chi^2_{(2)} = 1.35$; $p > 0.05$). Conversely, in MED, there were more phanerophytes than hemicryptophytes in unperturbed places (N, NR, R; $\chi^2_{(2)} = 8.32$; $p < 0.01$), whereas no significant difference was found in ATL ($\chi^2_{(2)} = 1.23$; $p > 0.05$).

3.2. Dispersal mode

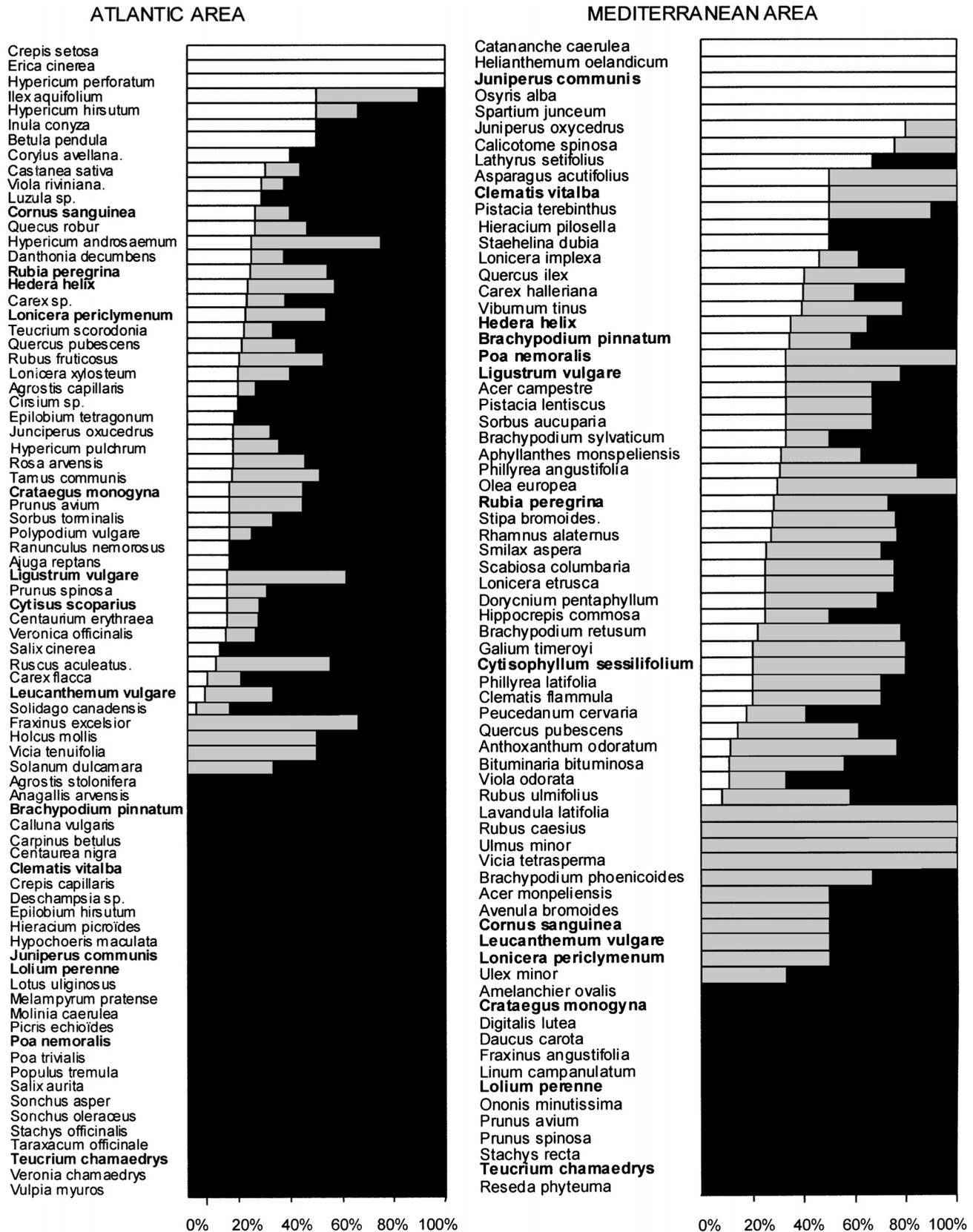
Epizoochory, was the least observed mode of dispersal in all ground surface types (Fig. 3), with only 6 species in ATL (*Brachypodium sylvaticum*, *Holcus mollis*, *Juncus conglomerates*, *Phleum pratense*, *Ranunculus nemorosus* and *Vulpia myuros*), and 2 species in MED (*Digitalis lutea* and *Galium timeroyi*). The category "other dispersal modes" (seeds dispersed by water, gravity and unknown dispersal modes) represented 21.1% of total species richness in ATL and 16.9% in MED. It appeared with more than 2 species in P, NP and RP in ATL, and in P and NP in MED; it was associated with perturbed places. Anemochory and endozoochory were the most observed dispersal modes in both studied areas; anemochory represented 49.5% of the total species richness in ATL and 38.0% in MED, while endozoochory represented 23.1% of the total species richness in ATL and 42.3% in MED. There were significantly more species characterized by anemochory in ATL than in MED ($\chi^2_{(2)} = 4.05$; $p < 0.05$), and significantly more with endozoochory in MED than in ATL ($\chi^2_{(2)} = 5.70$; $p < 0.05$). In ATL, anemochory was observed in N, P, NR, NP, and only one species in NRP, thus essentially in unperturbed and perturbed places. In MED, anemochory was observed in all ground surface types but it was more present in NP and RP. In ATL, endozoochory was higher in NP and P than in the other ground surface types. In MED, endozoochory was higher in P, NP and NRP.

3.3. Grime's strategies S, C and R

All the groups of species were characterized by competitive and stress tolerant (*CS*) strategies than ruderal ($R \leq 0.3$) (Fig. 4). In ATL, group species related to P (P, PR, NP) have high values for the sensibility to perturbation (*R*), group species related to R (R, NR, PR) have high values for the sensibility to competition (*C*) and group species related to N (N, NP, NR) had high values for sensibility to stress (*S*). In MED, group species related to P, PR and NR showed high value for perturbation (*R*), groups species related to PR, NR and NP showed high value for competition (*C*), and groups species related to N, R and NP showed high value for stress (*S*). Thus, in MED there was not one strategy (*S*, *C* or *R*) more associated with one ground surface type (P, R, N) than the others.

4. DISCUSSION

Analyzes carried out concerning effects of soil surface disturbances after logging on plant species diversity allowed us to confirm or partially confirm our three hypotheses. Hypothesis (1), that each soil surface disturbance type is characterized by a group of plant species, was verified. In the two areas, Atlantic



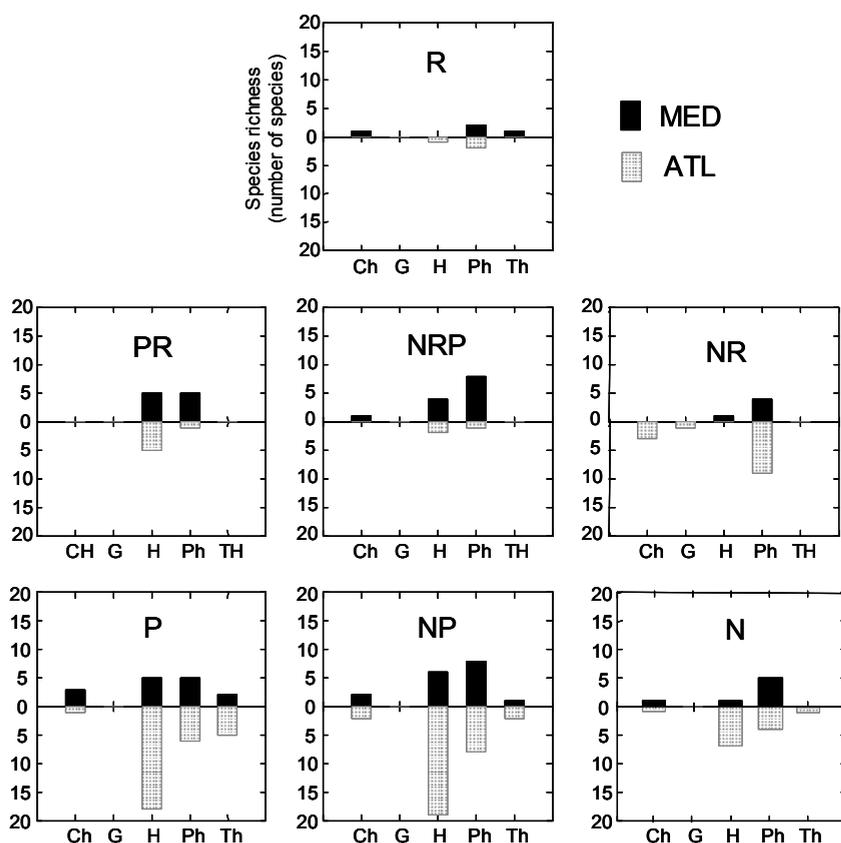


Figure 2. Species richness in terms of life forms defined by Raunkiær according to the group of affinity of the species for ground surface type and the area. ATL: Atlantic area, MED: Mediterranean area. Ch: Chamaephyte, H: Hemicryptophyte, Ph: Phanerophyte, G: Geophyte, Th: Therophyte.

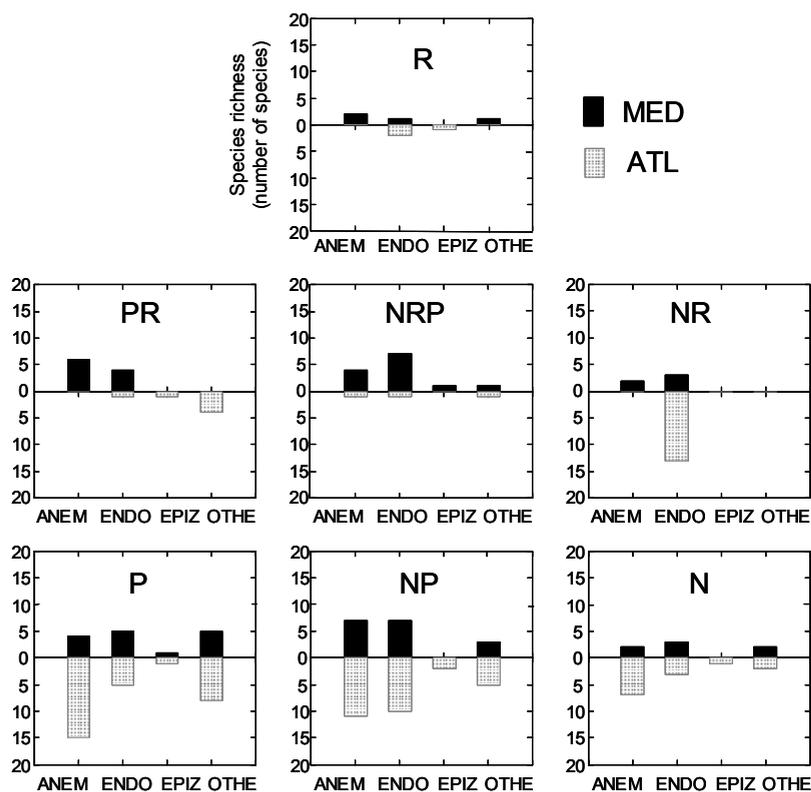


Figure 3. Species richness in terms of dispersal modes according to the group of affinity of the species for ground surface type and the area. ATL: Atlantic area, MED: Mediterranean area. Anem: anemochory; Endo: endozoochory and dispersal associated to animal feeding; Epiz: epizoochory; Othe: other or unknown dispersal modes.

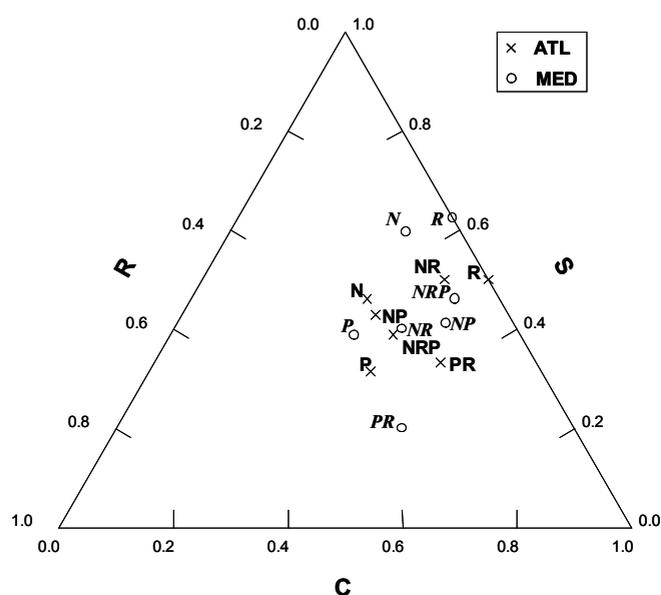


Figure 4. Mean position of the plant groups defined by their affinity to ground surface status in the Grime triangle defined by the sensitivity to perturbation (R axe), to competition (C axe) and to stress (S axe).

and Mediterranean, few species were observed when remnant depots were high, while many species were present in perturbed places and numerous species were associated with not perturbed places or were indifferent to perturbation. These results agree with many other studies showing that logging increases plant species diversity [32, 53]. However, plant species in the Mediterranean site had a lower affinity to ground surface types than in the Atlantic site. The low number of species associated with remnant depots can be explained by the fact that remnants compensate for canopy suppression due to logging by maintaining low light availability, high humidity and ample leaf litter [54]. Concerning the 14 species occurring in both the Atlantic and Mediterranean areas, only 6 species have similar trends with ground surface type. This variability in species response to perturbation could be explained by low plant species frequency. Moreover, all species which have been recorded in stands studied, which have been logged since less than 3 years, are common species. Analyses of vegetation composition in similar stands, logged since 30 years, also indicated that no rare species were observed in both area [13, 25]. Thus when canopy closes and species richness decrease, there are no rare species that enhanced conservation value.

Hypothesis (2), i.e., that groups of plant species have distinct biological traits, was partially verified. Indeed, the analyses showed that perturbed areas (P) were associated more particularly with hemicryptophytes, anemochorous and ruderal species; remnant depot (R) areas with seeds dispersed by animals and competitive species; and not perturbed (N) areas with seeds dispersed by wind or animals and stress tolerant species. There was no life form which characterized in particular R or N. As in previous studies [4, 20, 26, 28], we found that hemicryptophytes increased after logging and we specified here that they increased more particularly in perturbed

places. These plant species were essentially dispersed by wind and required perturbed areas, without litter, to germinate. Moreover, hemicryptophytes have a short life span and were probably not present in litter before logging. These forest and farm species probably arrived from the surrounding mosaic of forests and agricultural lands (essentially olive trees and vineyards in the Mediterranean area, and pastures and crops in the Atlantic area) [59]. Moreover, modalities of implantation of plant species depend on colonization pressure which is in turn heavily influenced by proximity to the logged forest. The temporal variation in plant diversity could also be analyzed. Indeed, plant diversity has been generally studied in relation to succession, few studies have addressed seasonal variation in plant diversity [but see 33, 67]. Concerning Grime strategies, plant species were globally speaking more competitive and stress tolerant than ruderal. This supposes that ground surface perturbations were so frequent and moderate that they were considered like a stress and not a perturbation by plant species.

The life traits selected in our study are relatively general, they synthesize other life traits as for example life forms that integrate both morphological and physiological criteria. But, all the possible life traits (leaf type, leaf consistency, nutrition type, vegetative multiplication etc.) were not available for the analysis because of lack of data on numerous species and also because of a discrepancy between the databases of life traits created separately in the two studies here compared. However, we found the same pattern in both areas, Atlantic and Mediterranean, for life forms and the dispersal modes; for Grime strategies, the species repartition in function of ground surface types was more stronger in Atlantic than in the Mediterranean area. Thus, hypothesis (3), that two different bio-geographic plant communities should have the same biological traits for a given soil surface disturbance, was not clearly verified. We conclude that life traits are a good tool to analyze ecosystem responses to disturbances such as logging. Expressing and grouping plant species primarily with regards their biological characteristics allows avoiding taxonomic attribution and thus, allows comparing result between two bio-geographic different sites.

The consequences of these sets of observations are that ground surface status influence plant species diversity. Thus, light availability and the related factors of moisture decrease, temperature modification, etc., cannot be considered as the only factor driving plant species diversity increase after logging. Moreover, the consequences of logging by different types of engines with increasing weight on the ground surface should be more carefully studied in order to be able to predict their influences on the vegetation.

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