

Combining plant and animal traits to assess community functional responses to disturbance

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There is a general consensus that functional traits are reliable indicators of adaptation of organisms to particular environmental characteristics. In this study we relate the combined distributions of species traits of plants and animals to disturbance regimes in chestnut forests of southern Switzerland affected by regular winter fires. We used co-inertia analysis for combining the trait response of 471 invertebrate species (117 001 individuals) and 81 plant species at 23 sites with different fire and cutting histories. Trait response was assessed by calculating the variation in weighted mean traits averaged over the communities and by using mean traits in multivariate analyses. The analysis showed a strong association between plant and animal traits under fire constraints (Monte-Carlo test, $p = 0.0045$). Plants and animal distributions show parallel trends in responses to fire which selects traits relating to persistence (ability to survive), resilience (ability to recover) and mobility. Warmth-demanding insects, herbivores, flying carnivores and pollinators were associated with recent fires, as were annual, ruderal and light-demanding plant species with long flowering duration. Small arthropods feeding on dead wood and those with narrow habitat requirements were associated with low fire frequency and unburnt sites, as were competitive plants with large seeds favoring moist sites. The spatial association between plant and animal traits reflected adaptations that promote survival in the disturbance regime, while the disturbance acts as an environmental filter on the distribution and assemblage of the trait values within communities.

This combined analysis of plant and invertebrate traits distributions illustrates how community and ecosystem responses can be monitored and the results generalized across localities and disturbance types. Analyses of traits that cross trophic levels provide powerful and promising tools for validating management procedures and controlling ecosystem functions.

The changes in ecosystem functions following perturbation are a central issue in disturbance ecology, and one of the most important forms of disruption is wildfire, often entailing extreme changes in environmental conditions, especially in forest ecosystems (Bengtsson et al. 2000 for review).

The effect of fire on plants and animals has often been studied at the taxonomic level. Predicting the functional responses of communities (e.g. services in pollination, biological control or biomass production) to environmental changes has, however only recently become a major concern in theoretical and applied ecological research (Lavorel et al. 1997, Hooper et al. 2005, Stillman and Simmons 2006). There is growing recognition that classifying organisms into functional traits and assessing changes in functional trait composition, in particular of traits related to dominant species, is a promising way forward for tackling important issues related to the functioning of the ecosystems (Lavorel and Garnier 2002, Schmitz 2003, Cornelissen et al. 2003, Garnier et al. 2004, Pausas et al. 2004, Díaz et al. 2007a, b).

Most studies in this direction have, however, been carried out only on plant traits, and included: broad-scale modelling of global vegetation (Wright et al. 2004, Smart et al. 2005); descriptions of the functional responses of a regional flora to environmental factors (Thuiller et al. 2004, Herault and Honnay 2005); and addressing specific disturbances (de Bello et al. 2005 for grazing; Pausas et al. 2006 for wildfire).

Animal traits have been less often used to study community response, and such studies have used just a few taxonomic groups and aspects of their ecology. Functional classifications of animals have been widely used in hydrobiological studies to assess the quality and the ecological value of aquatic systems (Devin et al. 2005, Statzner et al. 2005, Ilg and Castella 2006). In the case of terrestrial animals, ecological and functional traits have been used within single taxonomic groups, with species classified according to, for example, foraging strategies by spiders (Buddle et al. 2000); body size by hoverflies (Schweiger et al. 2007), or dispersion by carabid beetles (Ribera et al.

2001). Only few studies, to our knowledge, have so far used traits across widely different taxonomic groups and compared animal and plant traits (Hodgson 1993). Nevertheless, there is a general recognition that using traits across taxonomic groups can reveal new and interesting emergent ecological and functional properties across biomes and ecosystems, as well as animal-plant interactions.

Plants and animals have a long co-evolutionary history and their interactions are abundant and intriguing. They include exploitative, commensal, and mutualistic interactions, as well as those more related to the carbon and nutrient cycles (e.g. production, consumption, and decomposition). In several cases animal communities also respond to vegetation structure and habitat complexity (Moretti et al. 2002, Greenleaf and Kremen 2006) and these relationships are more likely to be revealed in functional trait data than in species compositional data.

In community assembly theory trait composition is seen to be largely determined by habitat filtering (Grime 2006, Cornwell et al. 2006). A set of environmental filters (e.g. climate, disturbance) act by selecting species with shared ecological tolerances (Díaz and Cabido 2001, de Bello et al. 2005, Grime 2006). There are multiple selective filters that act on the local species pool and most general adaptations are not specific to a single given environmental factor (Fonseca et al. 2000). In particular contemporary environmental filters can act either by selecting similar traits (convergence) or opposite traits (divergence; Grime 2006 for a review). For example, livestock grazing and aridity have convergent effects in selecting plant species with short life cycles (i.e. ephemerals) (de Bello et al. 2005), while divergent effect of rainfall and soil nutrient gradients on leaf size were observed by Fonseca et al. (2000) and McDonal et al. (2003) due to the broad range of physical conditions across microsites within each site and biotic interactions. Community responses to disturbance can therefore be of different extent in different regions (de Bello et al. 2005, Díaz et al. 2007b).

In this context, wildfires in chestnut *Castanea sativa* forests on the southern slopes of the Swiss Alps provide an ideal model system to test the functional response of animals and plants to post-fire changes. Tinner et al. (1999) suggest that southern Switzerland, like probably all of the southern slopes of the Alps, has been a fire-prone area since the Paleolithic.

In this study, we investigated the functional traits in communities of vascular plants and invertebrates during the post-fire succession. The aims were 1) to understand the extent to which the functional traits of the plant and animal species contribute to assessing post-fire successional patterns and 2) to detect relationships between the functional traits of post-fire successional vegetation and the associated invertebrate fauna.

The focus on functional traits provides, in a sense, a common “language” for making comparisons and building bridges across hierarchical levels. We therefore selected broad traits that can be easily assessed throughout the group, rather than those that may be specific to particular taxonomic groups. This results in a framework that is flexible enough to make comparisons at both the regional and global levels.

Methods

Study area and site descriptions

The investigation took place along a uniform, south-facing slope (450–850 m a.s.l.), extending over 11 × 15 km near Locarno (46°09'N, 08°44'E), Canton Ticino, in southern Switzerland. The study area has a moist, warm temperate climate, with rainfall higher in summer (June–September: ca 200 mm per month) than in winter (November–February: ca 100 mm per month) (Meteorological Station of Locarno-Monti; Spinedi and Isotta 2004). Thus the area is prone to fast-spreading surface fires of low-medium intensity, which occur during the period of vegetation dormancy (December–April) (Conedera et al. 1996). This results in a mosaic of burnt and unburnt areas, characterized by different fire frequencies and time elapsed since last fire. The vegetation is dominated by former coppice stands of European chestnut *Castanea sativa* on acid soil. The chestnut trees recover a full forest canopy within 20–30 yr after the fire, while the ground vegetation passes through several different successional stages. The forests have been regularly managed for about the last 2000 yr (since the Romans started cultivating chestnut in Europe), until the 1960s with a 20- to 30-yr cycle. Since then traditional management has stopped, but fire frequency has increased as the forests contain more potential fuel. More details of the study area are given in Moretti et al. (2002).

The sampling design was based on space-for-time substitution (Pickett 1989). The fire regimes of the study sites were classified in terms of fire frequency (number of fires recorded during the previous 30 yr) and age (time elapsed since the last fire). Other potential fire regime variables (e.g. type, season, intensity) vary very little across the study area.

The fire histories of the different sites over 36 yr (1968–2004) were mostly taken from the Wildfire Database of Southern Switzerland (Conedera et al. 1996) and dendro-chronological analyses.

We selected 23 sites grouped into three categories according to fire frequency: 1) six “unburnt sites”, where no fire had occurred for at least 30 yr served as control plots; 2) nine “single fire sites” where only one fire had occurred during the same period, and 3) eight “repeated fire sites” where either three or four fires had occurred since 1968. As far as possible, triplets of sites were chosen where a control plot, a “single fire site”, and a “repeated fire site” were in close enough proximity to assume similar environments. Then the composition of the vegetation and fauna of the control site could be considered original and the research design reasonably balanced. The sites were also selected to so that there would be a range of ages since the last fire (Table 1). At three sites the chestnut stands had also been completely coppiced by cutting at ground level.

Species and environmental data

Standard methods were used to collect the invertebrates: pitfall traps for sampling ground-dwelling arthropods, emergence traps for invertebrates emerging from the soil, and window traps for flying and flower-visiting species.

Table 1. Sites grouped into three categories of fire frequency: “Unburnt” as control, i.e. sites that had not been burnt in the previous 30 yr; “Single” and “Repeated fires” (3–4 fires) in the previous 30 yr. The last two categories were grouped according to time elapsed since the last fire; * indicates presence of one cut plot. Three sets of traps and quadrats were set up on each site.

| Fire frequency | Time elapsed since the last fire | | | | Control | Total |
|-------------------|----------------------------------|--------|---------|----------|---------|-------|
| | <1 yr | 1–3 yr | 6–14 yr | 17–24 yr | | |
| Unburnt (control) | | | | | 6 | 6 |
| Single fire | 1 | 2 | 3* | 3 | | 9 |
| Repeated fires | 1 | 2* | 4 | 1* | | 8 |
| Total sites | 2 | 4 | 7 | 4 | 6 | 23 |

The pitfall traps consisted of a plastic funnel recessed into the soil (diameter of opening 15 cm) and mounted on the top of a plastic bottle containing 2% formaldehyde solution. A roof 10 cm above the traps provided protection from the rain. The emergence traps consisted of a pyramid-like construction (50 × 50 cm at the base) fixed to the ground and covered with a fine black wire-mesh (mesh width <0.5 mm) to preserve the microclimatic conditions. Emerging insects were trapped in collection vials on top of the dark pyramid when they tried to escape to the light. The window traps were combined with a yellow water pan and placed 1.5 m above ground. For further details about the methods and their limitations, see Moretti et al. (2004).

On each of the 23 sites, three trap stations were installed, each consisting of a pitfall trap, an emergence trap, and a window trap, resulting in a total of 69 trap stations. The minimum distance between traps of the same type within each site was 10 m, while the average nearest neighbor distance between the sites representing the three treatments (no fire, single fire, repeated fires) within a group was 301 ± 128 m. The traps were emptied weekly from March to September 1997, which meant a total of 28 sampling periods covering the main activity season of most taxa.

Vascular plants were recorded using a seven-point species cover-abundance scale (Braun-Blanquet 1964) within a 10 × 10 m quadrat at each trap station, giving a total of 69 quadrats. The quadrats were recorded in May–June and again in August in order to identify as many species as possible and to include species with different phenologies. At the same time, four factors related to disturbance (i.e. fire and clear-cutting) and six site factors not directly related to disturbance (i.e. latitude and longitude, altitude, slope, aspect, soil texture) were assessed within the same quadrats (Supplementary material, Appendix 1). Secondary fire factors (environmental factors directly related to fire and cutting), such as vegetation and litter cover, were also recorded but not shown here (see Moretti et al. 2002).

Species traits

Selected families from six taxonomic orders of invertebrates (Isopoda, Aranea, Coleoptera, Neuroptera, Hymenoptera, Diptera) were identified to species level. Other invertebrates were recorded at a higher taxonomic level, but are not considered in this paper.

Each plant and animal species was described in terms of its functional traits to enable us to explore the mechanisms of community responses to disturbance and the nature of the associations between plant and animal communities. We selected twelve plant traits and seven animal traits

(Table 2). The animal and plant traits used are widely-used traits relevant to most taxa, and are based on well-articulated methodologies and consistent measurement.

Data analysis

Data analyses were designed to find relationships between functional traits and disturbance by fire, as well as between the responses of plants and animals to disturbance. Community compositions were examined at the functional groups level and at the species level, using species abundance data. The number of individuals of each species was log-transformed to reduce the effects of extreme values of the most mobile species that could have been overestimated by the use of interception traps. The 23 sites were tested for spatial independence of species assemblages using Mantel correlogram and permutation tests (Legendre and Legendre 1998). No significant spatial dependencies were detected (see Moretti et al. 2006 for more details) so the sites are treated as independent in the present analyses.

Primary data

The structure of the primary data comprises a number of linked matrices (Fig. 1). There were two species matrices, where Matrix A consisted of “species × sites abundance data” for the two species groups (plants and animals), and Matrix B of “species × traits data” for each species group, and four factor groups’ matrices: Matrix D consisted of “fire characteristics × sites” (time since last fire and fire frequency), Matrix E “cutting characteristics × sites”; Matrix F “site factors × sites”, and Matrix G “secondary fire factors × sites”. In the plant species × sites matrix (Matrix A), tree seedlings, saplings and canopy trees were treated as separate taxa (= plant types) because they were accepted to have different ecological responses to fire.

Derived data tables

Weighted averaging was used to combine the “species × sites” matrices (A) with the “species × traits” matrices (B) to obtain a mean trait score (T_m) for each site (Matrix C, Fig. 1), according to Garnier et al. (2004), as:

$$T_m = \sum_i p_i x_i$$

where x_i is the trait value of i -th species (for binary traits x_i can be either zero or one) and p_i is the relative abundance of the i -th species.

This generated new “traits × sites” matrices for each of the plant and animal data. The weighted averaging

Table 2. Description of plant traits (a) and animal traits (b). The columns with number of variables (No. var.) and datatype show how the data were used in the analysis. Thus maximum height is one ordinal variable with three categories; plant habitat was considered as a nominal variable and was therefore implemented as five “dummy variables”, each with two categories (present or absent); flowering phenology is two quantitative variables. Data were taken from numerous published sources, or from direct observation and from information obtained from the experts who had identified the specimens where published information for a particular species was not available.

| Trait groups | No. var. | Data type | Attribute |
|---------------------|----------|--------------|---|
| a) Plant traits | | | |
| Maximum height | 1 | 3 ordinal | MaxH: 1, herbs and sub-shrubs (≤ 150 cm); 2, shrubs (> 150 – 300 cm); 3, trees (> 300 cm) |
| Habitat | 5 | nominal | Most commonly present in: rocky areas (Rock); cultivated (Cult); meadow (Meadow); shrubland (Shrub); forest (Forest) |
| Flowering phenology | 2 | quantitative | FlowStart: flowering start (month); FlowDur: flowering duration (number of months) |
| Pollen vector* | 2 | nominal | Pollinated by wind (PollW); pollinated by animals (PollA) |
| Agent of dispersal | 2 | nominal | Zoochorous (Zooch); anemochorous (Anem) |
| Seed weight | 1 | 8 ordinal | SeedWeig: 0, no seed produced; 1, seed too small to be measured; 2, < 0.2 mg; 3, > 0.2 – 0.5 mg; 4, > 0.5 – 1.0 mg; 5, > 1.0 – 2.0 mg; 6, > 2.0 – 10.0 mg; 7, > 10 mg |
| CSR strategy | 3 | quantitative | Competitor (C); stress tolerant (S); ruderal (R) |
| Leaf persistence | 1 | 3 ordinal | LeafPer: 1, aestival green; 2, partial evergreen; 3, evergreen |
| Life history | 1 | 3 ordinal | LifeHist: 1, annual; 2, usually biennial; 3, perennial |
| Life form | 1 | 8 ordinal | LifeForm: 1, phanerophyte and nano-phanerophyte; 2, ph-ch; 3, chamaephyte; 4, ch-h; 5, bemicryptophyte; 6, h-g; 7, geophyte; 8, therophytes |
| Sprout insulation | 1 | 4 ordinal | SprIns: 1, vulnerable to fire damage; 2, moderately vulnerable; 3, moderately insulated; 4, well insulated |
| Lateral spread | 1 | 5 ordinal | LatSpr: 1, therophytes, lateral spread of exceedingly limited extent and duration; 2, perennials with compact unbranched rhizomes or forming small tussocks ($\varnothing < 10$ cm); 3, perennials with rhizomatous systems or large tussocks ($\varnothing 10$ – 25 cm); 4, perennials attaining $\varnothing 25$ – 100 cm; 5, perennials attaining $\varnothing > 100$ cm |
| Indicator values | 6 | 5 ordinal | Ellenberg et al. (1992) indicator values: humidity (F); reaction (pH); nitrogen (N); light (L); temperature (T); continentality (K) |
| b) Animal traits | | | |
| Body size | 2 | quantitative | Bodysize: absolute body length (in mm); %Bodysize: relative body length for each order where the largest species found in this study was scored 1.0. |
| Life form | 1 | 3 ordinal | LifeForm: 1, terrestrial; 2, terrestrial and aerial; 3, aerial |
| Trophic level | 6 | nominal | Ground dwelling carnivores (GrCarn); ground dwelling detritivores (Detritiv); flying carnivores (FlyCarn); herbivores (Herbiv); pollinators (Pollinat); myceto-saproxylous (Saprxyl) |
| Dispersal ability | 1 | 4 ordinal | Dispers: 1, absent or very poor; 2, medium; 3, good; 4, very good |
| Habitat requirement | 1 | 4 ordinal | Habitat: 1, open land; 2, forest edge; 3, open forest; 4, closed forest |
| Habitat specificity | 1 | 3 ordinal | HabSpec: 1, wide; 2, intermediate; 3, narrow |
| Temperature needs | 1 | 3 ordinal | T: 1, cold tolerant; 2, mesophilic; 3, thermophilic |

*For the purposes of this study ferns were included with wind-pollinated plants since the dispersal of spores that ensures genetic mixing is primarily through wind and no association with pollinating insects is expected.

procedure used the $\log(\text{count} + 1)$ transformation for invertebrate count data, and the seven-point Braun-Blanquet scale for plant abundance data.

Association between species and environmental variables

Detrended correspondence analysis (DCA) was first used for an initial exploratory analysis of the data (Step 1 in Fig. 1). Transformations were used, as appropriate, to reduce the effects of extreme values. Singletons, i.e. species that occurred in one sample only, were removed from all analyses of vegetation data, while invertebrate species represented by fewer than five individuals were excluded from all analyses of animal data. All analyses were conducted treating the 69 samples as independent replicates for all exploratory ordinations where the primary objective was pattern identification; the reasonably balanced design

ensures that environmental characteristics varying at the site level are not confounded by the main treatment effects (control, single or multiple fires). In all cases where significance testing was used the data were condensed to the 23 individual sites in order to avoid inflation of the type I error rate due to pseudoreplication (Hurlbert 1984). All analyses were performed with Canoco for Windows ver. 4.5 (ter Braak and Šmilauer 2002) unless otherwise stated.

Relationship between traits and factor groups

Three separate partial redundancy analyses (pRDA) were used to partition out the variance explained by the different factor groups (Borcard et al. 1992) for plant and animal traits separately (Step 2 in Fig. 1). These identified the relationships with the components of variation unique to: 1) the fire factors after removing the effects of cutting and

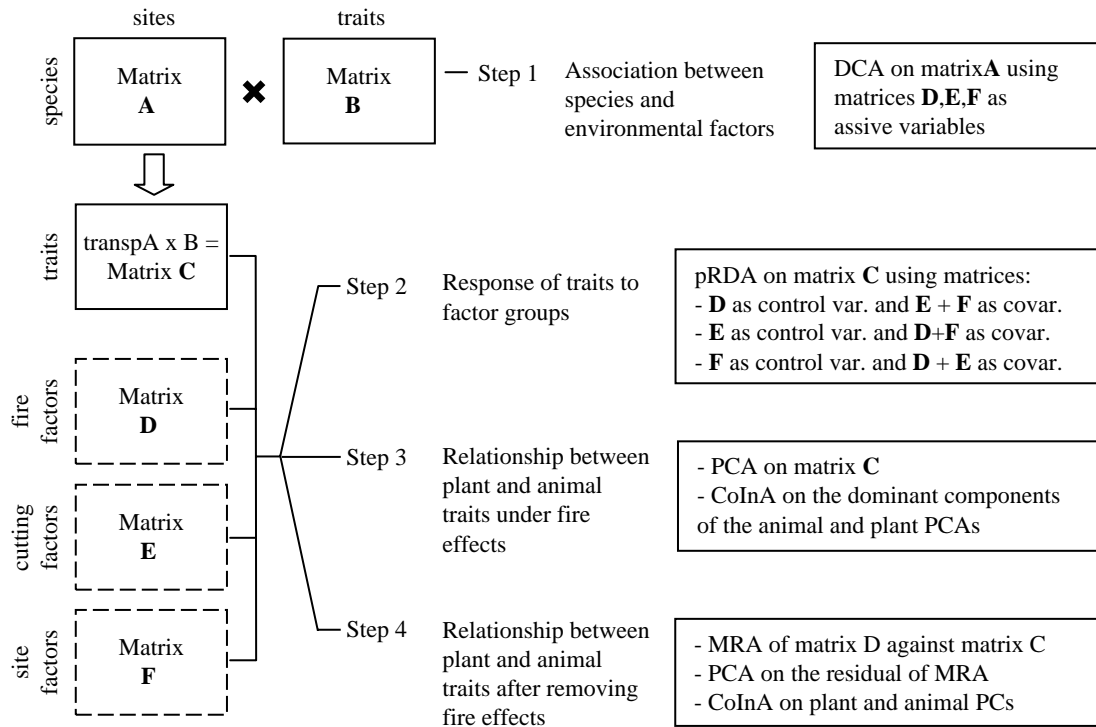


Figure 1. General design for the analysis. Species and trait matrices: Matrix A of species by sites, B of species by traits, C of traits by sites derived from A and B by weighted averaging; factor group matrices: Matrix D of fire factors by sites, E of cutting factors by sites, F of site factors by sites, G of secondary fire factors by sites. There were separate matrices A, B and C for plants and animals. Var. = variables; Covar. = covariables; DCA = detrended correspondence analysis; pRDA = partial redundancy analysis; MRA = multiple regression analysis; PCA = principal component analysis; CoInA = co-inertia analysis.

site factors as covariates (fire), 2) the cutting factors using fire and site factors as covariates (cut), and 3) the site factors using fire and cutting factors as covariates (site) (Supplementary material, Appendix 2).

Relationships between traits of plants and animals with post-fire succession

Co-inertia analysis (Dolédéc and Chessel 1994, Dray et al. 2003) was used to examine the association between plant and animal traits. The “traits \times sites” matrices (C in Fig. 1) were transferred to the statistical package R 2.3.1 (R Development Core Team 2006) and analyzed using the “ade4” package (Chessel et al. 2004). This involves first reducing the dimensionality of the plant and animal traits \times sites matrices using PCA and selecting the dominant components. New axes are then generated by rotation in multidimensional space so as to maximise the covariance between the new axes in the two datasets (Dolédéc and Chessel 1994) (Step 3 in Fig. 1). The significance of the association between the plant and animal traits was then tested with a Monte-Carlo permutation test.

In this analysis, both plant and animal distributions are strongly influenced by the fire frequency and fire age. A second co-inertia analysis was therefore performed using the two fire factors (D in Fig. 1) as covariables. This was achieved in R by regressing the trait data for each site (C) on the fire factors (D) and using the residuals in place of the trait data in the PCA as described above (Step 4 in Fig. 1).

Partial RDA and CoIA represent classical statistical methods widely used to analyse the relationship between species or trait matrices and environmental variables, or to compare the associated response of two matrices of different organisms, such as plants and animals (Dolédéc and Chessel 1994, Dray et al. 2003). Alternative methods such as RLQ analysis (Dolédéc et al. 1996) or fourth-corner statistics (Legendre et al. 1997) or double CCA (Lavorel et al. 1998) have been proposed. The latter method is a promising procedure for testing links between environmental variables and species traits that is used for presence-absence data. Since we are using abundances of species as important determinants of ecosystem function (Díaz et al. 2007a), we believe that our method is appropriate.

Results

The data sets

A total of 875 invertebrate species were identified from the 117782 individuals caught; 471 species (54%) were sampled with five or more individuals involving 117001 individuals (Supplementary material, Appendix 3). The mean species richness per site and per trap station was 224 and 147 species, respectively, while the mean number of individuals per trap was 1696. Ninety-four vascular plant species were recorded. Several plant species were recorded separately in the tree, shrub and herb strata, amounting to a

total of 120 recorded plant categories. We refer to these as plant types. Eighty-one species (102 plant types) sampled on at least two sites were used in the data analyses (23 types were recorded on average per site, and 20 types per station; Supplementary material, Appendix 3).

Relationship between species and environmental factors

An initial inspection of the vegetation data using DCA (Supplementary material, Appendix 4) showed relatively weak patterns of species distribution with the first two axes representing 16% of the species variation. The axis lengths were about 2.4 standard deviations. With plants, the first axis separated rather closed from more open sites. The former had mostly intact and late successional stage forests with a closed and diverse tree canopy (e.g. *Castanea sativa* woodland with one or more of: *Prunus avium*, *Robinia pseudacacia*, *Tilia cordata*, *Sorbus aria*) as well as shade tolerant and evergreen species (e.g. *Hedera helix*, *Prunus laurocerasus*, *Trachicarpus fortunei*, *Dryopteris borreieri*). The other sites tended to have been recently and frequently burned, and to be found at higher altitudes with more open canopies (e.g. *Quercus petraea*), as well as a denser grass and bush cover. The first axis reflected the variation in both altitude and fire frequency and hence time since last fire. The second axis tended to divide sites with more recent fires into those at low altitudes where fire is infrequent (sites with abundant dead wood and large trees, *Anemone nemorosa*, *Silene dioica* and *Viola riviniana*) and those at high altitudes where fire has been more frequent (more open, grassy vegetation with *Festuca ovina*, *Galium verum*, *Silene vulgaris*).

DCA performed on the “invertebrates \times site” matrix (Matrix A) also showed relatively weak gradients with the first two axes representing 16% of the variation and the gradient length about 1.5 standard deviations (Supplementary material, Appendix 4). In this case the first axis was strongly correlated with time since last fire and cutting. The control sites (not burnt or cut for at least 30 yr) were clustered at one end of the first axis and hosted ground-dwelling and epigeic species (e.g. ants, spiders, weevils, carabids, and other beetles), while sites burned within the last two years were characterized by highly mobile invertebrates, particularly flying species (e.g. bees and wasps), at the opposite end. The second axis separated the more sunny and recently cut sites on S/SW-facing slopes from sites on slopes with denser coppice stands. The percentages of variance explained by the first two axes and by all axes were similar for plant and animal communities.

Relationship between traits and factor groups

Plant traits were found to be significantly associated with fire factors after removing the co-variance of the cutting factors and the site factors in the pRDA (Table 3a). The two fire axes explained 27% of the remaining variation. Time since last fire correlated with both the first and second axes, while number of fires was highly correlated only with the second (Fig. 2a). Clear-cutting showed a significant relationship with the first axis of the plant trait data after

removal of the covariables, while the site factors did not show any significant relationship after removing both fire and cutting as covariables.

The results with animal traits in the first pRDA (Table 3b) were similar to those with plant traits, i.e. there was highly significant association between the trait data and fire occurrence, and a high correlation between time since last fire and both axes, as well as between number of fires and the second axis (Fig. 2b). The two axes explained 46% of the variance. Both clear-cutting factors were highly correlated with the first axis of the pRDA, explaining 28% of the variance. Among the remaining factors, on the other hand, only altitude and longitude correlated with the first axis of the last pRDA.

The pRDA for plant and animal traits (Fig. 2a, b) revealed the relationship between traits and fire. A group of ten plant traits (Supplementary material, Appendix 5a and 6) were associated with recent fires. These traits correspond to annual plant species living in mesic shrublands, especially ruderal geophytes and therophytes with long flowering duration, pollinated by insects, and dispersing seed by wind (they therefore had very light seeds). Plant species tolerant of high temperatures increased with frequent fire, while shade-tolerant plants increased with time since fire and to be more abundant on single-fire sites than frequent-fire sites.

For animal traits (Supplementary material, Appendix 5b and 7), recent fires and, to a lesser extent clear-cutting, favored open-land, thermophilous pollinators and therefore species with a high flight capacity living in an aerial landscape. On the other hand, ground-dwelling carnivores and detritivores were negatively affected by recent fires and clear-cutting. Species feeding on wood and fungus on trees (myceto-saproxylrophagous) were negatively affected by increasing number of fires, while clear-cutting negatively affected herbivores and species with narrow habitat requirements.

Relationships between traits of post-fire successional plants and animals

Inspection of the eigenvalues and a scree plot of the initial PCA of the “plant traits \times sites” matrix (C in Fig. 1) highlighted seven eigenvectors (representing 88% of the variation) to be used in the co-inertia analysis for comparison with the animal traits. Similarly, four eigenvectors with eigenvalues were selected from the PCA of “animal traits \times sites” matrix (C in Fig. 1) representing 89% of the variation. Co-inertia of the simplified seven- and four-dimensional data showed very high association between these two datasets ($p = 0.0045$, Monte-Carlo test based on 9999 permutations).

Co-inertia analysis (Fig. 3c) shows that the first principal components of the PCA on animal (Fig. 3a) and plant traits (Fig. 3b) are strongly associated and dominate the co-structure of the two datasets; the first eigenvalue represents 78% of the co-structure and the second 9%. The first axis of the co-inertia analysis clearly relates to the fire history of the sites: plots on the left of the ordination (Fig. 3c) represent recent fires and those on the right the control sites and more mature stands. The second axis separates the sites

Table 3. Partial redundancy analyses (pRDA) of the plant (a) and animal (b) traits for 23 sites in the environmental space (explanatory factors): fire, cut, and site (see Methods and Supplementary material, Appendix 2). Coeff = correlation coefficient between the factors and the first two axes of the three pRDA. The variable names are defined in Table 2; % Variance explained = variance of the trait-environment relationship in%. P indicates the Monte Carlo test of significance of the first and of all axes (n = 9999).

a) Plants

| Factor groups | Explanatory factors Covariables | Fire cut, site | | Cut fire, site | | Site fire, cut | |
|-----------------|--|--------------------------|-------------------------|--------------------------|-------------------------|--------------------------|--------------------------|
| | pRDA axes | axis 1 | axis 2 | axis 1 | axis 2 | axis 1 | axis 2 |
| | Eigenvalues % Variance explained Factors | 0.180 30.9 Coeff 1 | 0.044 7.6 Coeff 2 | 0.044 10.3 Coeff 1 | 0.024 5.7 Coeff 2 | 0.088 14.7 Coeff 1 | 0.070 11.8 Coeff 2 |
| Fire factors | Nfire | −0.081 | −0.810 | | | | |
| Cutting factors | Tfire | 0.792 | 0.453 | | | | |
| | Cut | | | 0.781 | −0.149 | | |
| | Tcut | | | −0.794 | 0.089 | | |
| | CoordX | | | | | 0.080 | 0.278 |
| Site factors | CoordY | | | | | 0.360 | 0.020 |
| | Alt | | | | | −0.220 | −0.340 |
| | Asp | | | | | −0.229 | −0.049 |
| | Slope | | | | | −0.352 | −0.601 |
| | Soil | | | | | −0.008 | 0.285 |
| | p | 0.004 | 0.129 | 0.420 | 0.647 | 0.258 | 0.247 |
| | p (all axes) | 0.002 | | 0.341 | | 0.096 | |

b) Animals

| Factor groups | Eigenvalues % Variance explained Factors | 0.184 35.3 Coeff 1 | 0.054 10.4 Coeff 2 | 0.104 26.5 Coeff 1 | 0.006 1.5 Coeff 2 | 0.132 26.1 Coeff 1 | 0.059 11.8 Coeff 2 |
|-----------------|--|--------------------------|--------------------------|--------------------------|-------------------------|--------------------------|--------------------------|
| Fire factors | Nfire | 0.196 | −0.712 | | | | |
| Cutting factors | Tfire | 0.532 | 0.575 | | | | |
| | Cut | | | 0.804 | −0.021 | | |
| | Tcut | | | −0.798 | −0.070 | | |
| | CoordX | | | | | −0.457 | −0.246 |
| Site factors | CoordY | | | | | −0.341 | −0.522 |
| | Alt | | | | | −0.826 | 0.090 |
| | Asp | | | | | 0.183 | 0.248 |
| | Slope | | | | | 0.246 | −0.290 |
| | Soil | | | | | 0.328 | 0.138 |
| | p | 0.002 | 0.031 | 0.015 | 0.696 | 0.031 | 0.717 |
| | p (all axes) | <0.001 | | 0.030 | | 0.078 | |

with repeated fires from control sites or those that have only experienced a single fire in the previous 30 yr.

This analysis clearly shows the nature of the association between the traits and fire. Thermophilous insects, herbivores, flying carnivores and pollinators tend to be associated with recent fires, along with annual, ruderal and light-demanding plant species with long flowering duration. On the second axis, control sites and sites with single fires are associated with small myceto-saproxylphagous insects and invertebrates with narrow habitat requirements, and with competitive plants with large seeds favoring moist sites.

Removal of the fire variables as covariates from the trait data again resulted in seven eigenvectors being selected from the PCA of the plant traits and four eigenvectors from the animal trait data. However, co-inertia analysis failed to find any significant association between the resulting principal components for the plant and animal traits ($p = 0.22$). This implies that there is no detectable association between plant and invertebrate traits at the site level other than that which can be explained by their joint response to fire.

Discussion

Response of species and traits to fire and clear-cutting

Our results showed parallel changes in species composition following fire and clear-cutting in plants and animals. Nonetheless, there was a higher turnover of plant species on the first axis of the DCA (2.5 standard deviations) than on the equivalent axis for animals (1.5 standard deviations). This difference may reflect narrower niches of plants with respect to the post-fire successional gradient, or the greater mobility of animals enabling them to colonize new habitats more rapidly.

From the functional point of view, our findings show that fire and clear-cutting selected particular traits in both plant and animal communities. Changes in environmental conditions following disturbance have filtered traits (Díaz et al. 2007a for review), determining which traits and functions can survive at any particular site (Lavorel et al. 2007).

The ability to resprout, to compete and to disperse that characterize the response of the dominant plant species to disturbance in our study are important life-history traits

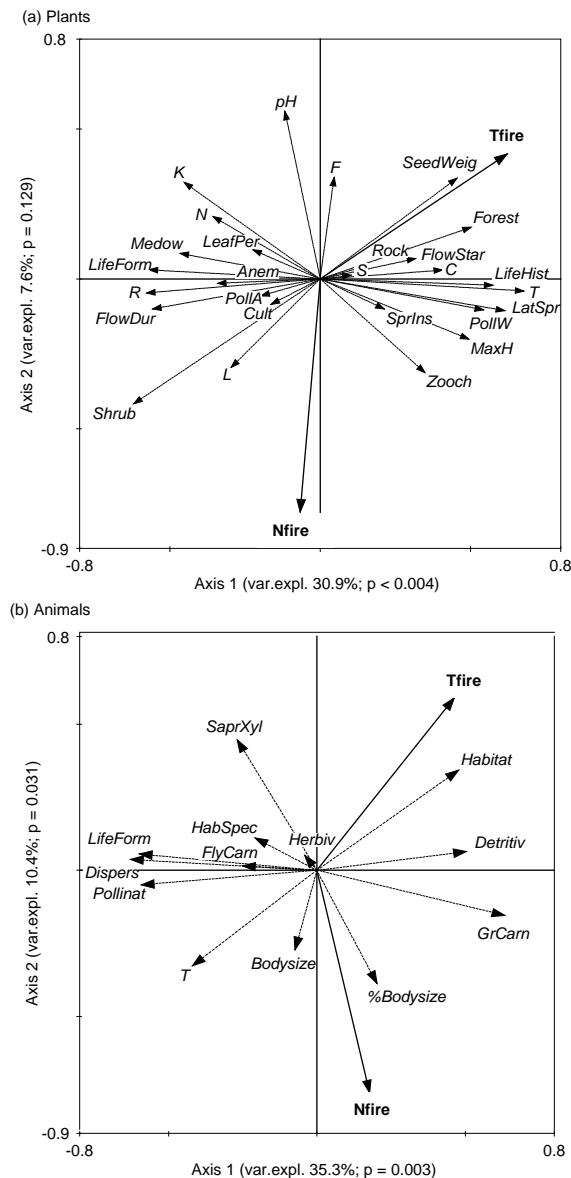


Figure 2. (a–b) Biplots of the partial redundancy analysis (pRDA) for plant (a) and animal (b) traits (dotted arrows; see Table 2 for trait names) for 23 sites in the fire space, where fire factors (continuous arrows; Nfire = number of wildfires in the previous 30 yr; Tfire = time elapsed since the last fire) were used as explanatory variables, and cutting and site factors (Supplementary material, Appendix 1) as covariables. See also Supplementary material, Appendix 6 and 7.

related to post-fire persistence in many ecosystems throughout the world (Pausas et al. 2006). Among animal traits, body size, flying ability, position relative to the ground (life form), and trophic guilds have been found to be the functional traits most affected by disturbance and land-use changes (Discroll and Weir 2005).

Nonetheless, we found that the overall functional responses to fire and clear-cutting were different in our analyses, particularly for plants, highlighting that the dynamics associated with clear-cutting do not mimic those associated with fire, at least at the functional level (Gallant et al. 2003). While both fire and cutting affect plants directly

by reducing above-ground biomass, fire induces physical and chemical changes to the soil that may be important throughout the post-fire succession. It is not surprising that fire selects plant traits related to the physical-chemical soil properties by promoting low-nitrogen and drought-tolerant species, as well as species adapted to a continental climate which can tolerate fluctuations in temperature.

Fire seems also to be associated with reproductive plant traits (e.g. longer flowering duration at burnt sites) and the dispersal of propagules. Species with light seeds are the earliest to colonize (Pausas and Lavorel 2003). Wind pollination is more effective than insect pollination in intact closed forests since most insect pollinators need open stands or gaps where sunlight penetrates the canopy.

Clear-cutting, on the other hand, removes the shrub layer but does not eliminate saplings or the thin-barked trees that are killed by fire. Competitors and heliophilous species are favored, while the litter and herbs remain mostly intact. Clear-cutting and fire both select traits that are likely to be related to early stages of post-disturbance succession. Shade-tolerant species were replaced by species living in open habitats, while large pluriennial phanerophytes were replaced with small herbaceous geo- and hemicryptophytes, as Gondard and Romane (2005) also observed shortly after chestnut coppicing in southern France.

Flying and warmth-demanding insects appeared to take advantage of the early successional stages following fire and clear-cutting in chestnut ecosystems, while small ground-dwelling predators and decomposers were clearly more directly affected by the reduction in litter and old dead wood, and were unable to recolonize from the surrounding intact areas.

Associated functional responses of plants and animals to disturbance

The co-inertia analysis showed a strong association between plant and animal traits under fire constraints. Traits associated with dispersal (e.g. seed weight in plants; body size and dispersal ability in animals) and pioneer habitats (e.g. ruderal plants and warmth demanding invertebrates both living in open habitats) were selected by fire in both plants and animals. These traits allow colonists to take advantage of the early successional resources and new habitat conditions. This suggests that disturbance by fire induces a convergent selection of the plant and animal traits mainly associated with persistence (ability to survive) and resilience (ability to recover) (Pausas and Lavorel 2003, Pausas et al. 2006). We believe that fire acts as a convergent environmental filter on plants and animals selecting the traits most suitable to fire and post-fire conditions (McDonal et al. 2003).

Animal traits associated with dispersal ability were strongly correlated with primary food availability and habitat conditions, as well as with the life history and life form of plants along the gradient of time since last fire. Pollinators were not only obviously associated with the flowering plant species, but the highly mobile species (mainly large bees) were able to exploit the longer flowering duration of ruderal hemicryptophytes and geophytes at recently burnt sites. The less mobile and moisture-demanding ground-dwelling

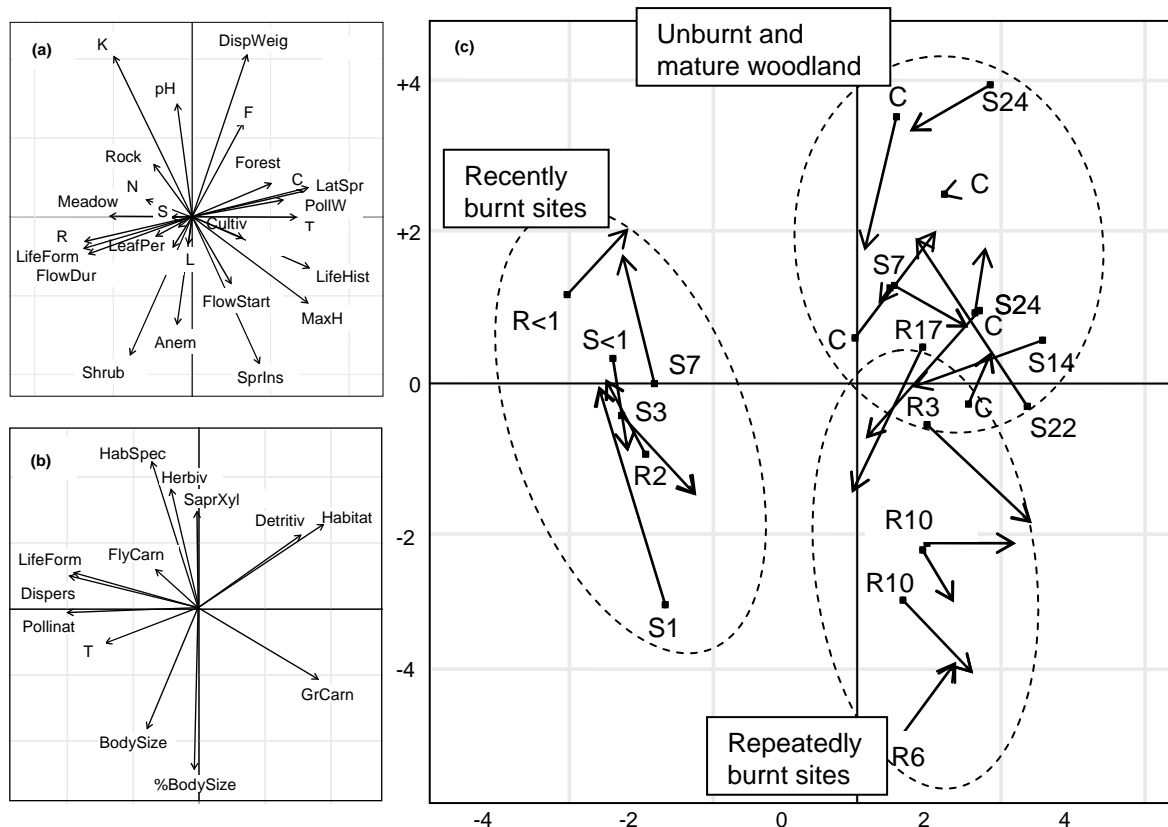


Figure 3. Co-inertia analysis comparing the distribution of animal and plant traits (see Table 2 for trait names): relationship between plant traits (a), animal traits (b) on the new ordination axes; (c) ordination of sites based on plant traits (base of arrow) and animal traits (head of arrow) in the new ordination space. Short arrows indicate that the plant and animal traits occupy similar positions in the ordination space; (S = single fire site; R = repeated fires site; the number indicates the number of years elapsed since the last fire; C = control site unburnt for at least 30 yr).

invertebrates and wood-eating insects, on the other hand, were negatively affected by the reduction in litter and dead organic matter arising from the loss of plant cover. Although the early resprouting plant species, such as chestnuts, ferns and *Molinia* recover quickly, the litter layer remains sparse, unstructured, and only loosely bound together due to the lack of cohesion between the layers. The wood-eating arthropods, particularly those living on the ground, are dramatically reduced in biomass by fire (Moretti et al. 2004) and communities take > 24 yr after the last fire to recover (Moretti et al. 2006). Our results show a marked relationship between the selection of saproxylic invertebrates, plant life history (i.e. decrease of perennial plants following fire) and maximum height (i.e. changes in vertical vegetation structure by a decreasing in shrubs and trees) following the fire, with a decrease of several woody species that are sensitive to fire (Tinner et al. 1999). Early successional stages in boreal forests are favorable to a high number of early successional wood eating species (Sippola et al. 2002). This positive effect is limited in chestnut dominated forests due probably to the high tannin content of the chestnut wood that limits decomposition and diversity in woody debris. The positive association between saproxylics and ruderal light-demanding plant species living in meadows can instead be explained by the fact that several wood-eating species forage on flowers (nectar) during the adult stage and lay eggs in sunny exposed places at the forest margins and in gaps.

Small-seeded plants and highly mobile large insects were both favored by more frequent fire, indicating a common response to disturbance. At frequently burnt sites, light seeds give plants the advantage of being able to disperse over long distances (Westoby et al. 1996). Small seeds may also be associated with dormancy, which facilitates survival of disturbance events in the soil seed bank (Thompson and Grime 1979). The large arthropod species typical of forest margins, gaps, and shrubland move quickly into the burnt sites taking advantage of the new environmental conditions and resources better than smaller species with narrower habitat requirements that are better able to exploit resources on a smaller spatial scale. On the other hand, sedentary decomposers and saproxylics, particularly those typical of stable habitats, have difficulty surviving on burnt sites (Moretti et al. 2006).

Overall, the association between plant and animal traits decreased after removing the effect of fire from the co-inertia analysis. This reflects the strong influence of disturbance on the selection of the functional traits of species on the southern slopes of the Alps where there has been a long history of fire and intensive clear-cutting (Tinner et al. 1999). This might act as an environmental filter sensu Díaz et al. (1998) and Cornwell et al. (2006) on the distribution and assemblage of the trait values within communities. This pattern is consistent with that found by de Bello et al. (2005), who studied the effects of grazing

along a climatic gradient in the Mediterranean. They claim that strong selective filters at the species and functional levels, such as chronic disturbance by grazing and fire, can limit the ability of communities to respond to other environmental factors.

Implications for monitoring community change and conclusions

Our study has demonstrated complementary patterns in the traits of animals and plants in mobility, use of resources and reproduction in response to woodland disturbance. **Animal traits often provide a functional parallel to the change in plant traits, which are related to important ecosystem processes and services such as pollination, trophic transfer, nutrient cycling, etc. (Díaz et al. 2007a). Despite the paucity of information on functional traits, particularly for animals, the combined analyses of plant and animal traits can yield the information necessary to predict the effect of various types of disturbance from a functional perspective (Gondard et al. 2003).** This would allow us to develop models that could be used to plan and predict trends in ecosystem evolution, assess ongoing processes, and monitor community and ecosystem responses to management practices. Nevertheless, we believe that there is an urgent need to further validate the **ecological and functional mechanisms related to animals and animal-plant interactions in order to identify sensitive and reliable indicators of ecological processes.** Such indicators would provide powerful and promising tools for validating management procedures and controlling ecosystem functions, and would give understanding of global change drivers and their effect on ecosystem functioning and ecosystem services.

Acknowledgements – We are grateful to Jan Lepš and Francesco de Bello for useful comments on the manuscript and to S. Dingwall for helping to revise the manuscript. Many thanks are due to the people who helped with the fieldwork (P. Wirz, F. Fibbioli) and to those who identified or checked the species (F. Amiet, S. Barbalat, R. Bärffuss, G. Carraro, P. Duelli, C. Germann, I. Giacalone, A. Hänggi, X. Heer, P. Hördegen, O. Stucky, D. Wyniger, P. Zahradnik).

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