

Functional traits and local environment predict vegetation responses to disturbance: a pan-European multi-site experiment

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Summary

1. Disturbance is one of the most important factors structuring the taxonomic and functional composition of vegetation. Vegetation resistance or resilience to disturbance depends on local environmental conditions, further modifying the pool of species and traits. This paper aims to understand how disturbance and local environment combine to affect the resistance and resilience of vegetation.

2. A functional-trait approach was used to detect traits related to vegetation resistance and resilience, and trait attributes of individual species responding to disturbance. Trait approaches enable comparison of vegetation responses across biogeographic regions containing different species pools.

3. At 35 European forest and grassland sites, experimental disturbance (human trampling) was applied at five intensities. Indices for resistance and resilience were calculated, based on total vegetation cover, and related to climate and local site factors. Additional indices were calculated for the most common species to demonstrate traits that confer resistance and resilience to disturbance.

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4. Vegetation resistance was related to occurrence of species with traits selected by a history of intensive land use (smaller leaf size, rosette plant form) and local environmental conditions. Vegetation resilience, however, was associated with ecosystem properties that facilitate higher growth rates. Resilient vegetation occurred where irradiation was higher (grasslands, open forests) with sufficient water availability (summer precipitation, humidity) and comprised of species with traits related to enhanced growth rates (increased specific leaf area, decreased leaf dry matter content).

5. *Synthesis.* This pan-European disturbance experiment demonstrates that different drivers (land use or climate) of vegetation response show different mechanistic responses to physical disturbance. Resistance depends on the functional composition of predominant species in the assemblage, which is strongly affected by land-use history; resilience is directly connected to growth rates affected by climate. We argue for the inclusion of land-use history and climate into the planning process for visitor management, especially in areas of high conservation interest.

Key-words: aridity, climate, continentality, determinants of plant community diversity and structure, forest, grassland, hemeroby, plant ecological strategy, resilience, resistance

Introduction

Disturbance is one of the most important factors structuring communities in terrestrial ecosystems (Pickett & White 1985; Papaik & Canham 2006). A particular disturbance regime – comprising disturbance type, intensity, frequency and severity – will lead to a specific plant assemblage with traits pre-adapted to this disturbance regime. Several ecosystem functions (e.g. nutrient storage, productivity) and properties (e.g. species composition or population structure) are determined by the current disturbance regime (de Grandpre & Bergeron 1997; Herbert, Fownes & Vitousek 1999; Papaik & Canham 2006; Bruelheide & Luginbühl 2009). Consequently, the disturbance regime (intensity, frequency and quantity) plays an important role in the community assembly and development of ecosystems (Turner *et al.* 1998; Römermann *et al.* 2009).

Under a given disturbance regime, vegetation development is additionally influenced by several abiotic and biotic factors. There are many studies describing the effect of water availability or irradiation on vegetation development within different ecosystems (e.g. Dzwonko & Loster 1997; Gallet & Roze 2001), and others have related resistance and resilience to specific plant communities and environmental gradients (e.g. Grime 2001). Resistance is the ability of the vegetation to withstand disturbance, whereas resilience is the ability to recover to the pre-disturbed state. However, only few studies exist relating resistance and resilience across a broad range of vegetation types and environmental factors such as climate (e.g. Hill & Pickering 2009; but compare Grime 2001; who placed plants along gradients of physical and physiological stress with ruderals lying at the extreme end of the physical stress gradient). The relative lack of such generalized studies may be because persistence of a population in a disturbed habitat depends on the frequency and severity of the disturbance events and as such needs much data (Turner *et al.* 1998).

Beside natural disturbance, in recent decades the anthropogenic pressure on natural or semi-natural habitats has

increased. In nature reserves or national parks, for example, a substantial increase in visitor numbers has increased disturbance by trampling from recreational activities such as hiking or dog walking (e.g. Monz 2002; Kerbiriou *et al.* 2008). Thus, in this study we focus on the effects of human trampling on the resistance and resilience of forest and grassland vegetation.

We applied standardized experimental disturbance by human trampling systematically at different intensities to the vegetation of the herb layer across a range of ecosystems.

Trampling is known to drive changes in plant community composition and structure (Cole & Bayfield 1993; Gomez-Limon & De Lucio 1995; Willard, Cooper & Forbes 2007; Forsberg 2010). Disturbance by trampling mainly affects vegetation directly by damaging plant tissues (Bates 1935), and indirectly by modifications to soil structure (e.g. Roovers, Gulinck & Hermy 2005), water regime (Kozłowski 1999), and nitrogen mineralization (e.g. Breland & Hansen 1996). Other evidence indicates that the effects of trampling on soil compaction remain unclear (Cole 1987; Lei 2004; Amrein, Rusterholz & Baur 2005) or at least are important only in areas of chronic disturbance (long-term effect, Kissling *et al.* 2009). For single disturbance events, the direct effects of the damage to plant tissues are generally most important (Roovers, Gulinck & Hermy 2005). It is possible, therefore, that the general pattern, if not magnitude, of vegetation response to disturbance by intensive human trampling will hold for other disturbances (e.g. cattle grazing) that damage plant tissues and soil structure.

The resistance and resilience of plant species to disturbances, such as trampling, is strongly associated with the morphological characteristics of those species (e.g. Del Moral 1979; Bratton 1985; Roovers, Baeten & Hermy 2004). Life-form and plant height are often good predictors of plant community responses to trampling (Sun & Liddle 1993; Roovers, Baeten & Hermy 2004). Thus, a plant functional-trait approach may be useful to discover generic patterns and processes underlying vegetation changes triggered by disturbance. For this, plants

with similar ecological traits are assumed to respond to environmental change in comparable ways (McIntyre, Lavorel & Tremont 1995). A functional-trait approach can reveal mechanistic shifts in vegetation arising from altered management (Lavorel *et al.* 1997; Fortunel *et al.* 2009), environmental conditions (MacGillivray *et al.* 1995; Bernhardt-Römermann *et al.* 2010) or succession (Garnier *et al.* 2004; Bernhardt-Römermann *et al.* 2008). Moreover, a functional-trait approach helps comparing vegetation responses across biogeographic regions containing different species pools (Diaz *et al.* 2004).

To predict plant species responses following disturbance it is necessary to consider species relationships to the current abiotic (e.g. soil, climate) and biotic (e.g. competitors) environment. The assembly of the vegetation in disturbed habitats will be determined by the adaptive strategies in the local species pool (Roovers, Baeten & Hermy 2004). Thus, differences among ecosystem (e.g. heathland, forest or grassland) responses may be explained by varying community composition, because the potential for resistance or resilience depends on the functional composition of the predominant species (Cole 1987; Arnesen 1999; Roovers, Baeten & Hermy 2004). Perennial species with the ability to re-sprout (like *Deschampsia cespitosa* or *Poa pratensis*) are likely to be more resilient than annuals (Roovers, Baeten & Hermy 2004). Hemicryptophytes have a greater ability to recover than chamaephytes (Andrés-Abellán *et al.* 2006). In general, plants with higher growth rates are predicted to have greater resilience (MacGillivray *et al.* 1995; Fortunel *et al.* 2009). The ability to resist single disturbance events is strongly related to life-form characteristics. Juvenile phanerophytes and chamaephytes, with their buds at a distance from the ground, are more sensitive to trampling than hemicryptophytes or geophytes that have their buds at or below-ground level (Liddle 1975; Roovers, Baeten & Hermy 2004); rosette plants are less sensitive than erect ones (Cole 1995).

Thus, we can expect that ecosystems where vegetation has a history of frequent disturbance (e.g. grasslands contain species possessing adaptations enabling persistence under grazing or mowing pressure) will be more resistant and resilient to disturbance than ecosystems where regular and intense disturbances are uncommon (e.g. semi-natural forest understoreys may be less adapted to intense disturbance).

Even within the same ecosystem type, the ability to withstand disturbance events is likely to be depend on nutrient (MacGillivray *et al.* 1995) and water availability (Cole 1995; Gallet & Roze 2001). Some ecosystems adapted to drought are known to be very resistant to trampling (Andrés-Abellán *et al.* 2006), while in general wet habitats seem to be most sensitive (Grime & Campbell 1991; Francis *et al.* 2005). Thus, resistance and resilience both show differences across climatic (Liddle 1975) and elevation gradients (Gomez-García, Azorin & Aguirre 2009).

This paper presents the results of a pan-European controlled experiment (35 sites across 10 countries) to establish how plant community responses to disturbance frequency are affected by ecosystem type (forest or grassland), climate, background

anthropogenic disturbance or hemeroby (hemeroby is somewhat analogous to the degree of 'naturalness'), and site conditions (e.g. elevation, soil). This paper will test the following hypotheses:

- 1 Ecosystems with higher levels of background anthropogenic disturbance will be pre-adapted and thus be more resistant and resilient to experimental human trampling.
- 2 Climate and local site factors will modify vegetation resistance and resilience to trampling, both of which should be lowest in wet habitats, fertile soils and at low elevations.
- 3 Plant functional traits (e.g. growth form) will predict vegetation resistance and resilience. Perennial plants with the ability to re-sprout and species with high growth rates will have high resilience, while slow-growing plants with below-ground buds will have high resistance.

Materials and methods

EXPERIMENTAL DESIGN

In 10 European countries we established a total of 35 experimental sites either in grassland ($n = 15$) or forest ($n = 20$) ecosystems (Table 1). Disturbance was applied as systematic human trampling of the field layer vegetation at standardized disturbance intensities following a protocol recommended by Cole & Bayfield (1993).

Four replicate blocks, each consisting of five experimental plots, were established in 2007, resulting in 20 experimental plots per site. Each plot was 0.5-m wide and 2-m long and slope was zero or negligible. Between the plots, a buffer zone of at least 0.5-m width was left to avoid the effect of adjacent treatments. Treatments were assigned randomly to the plots of each block comprising an undisturbed control (zero trampling) and experimental disturbance intensities applied as 25, 75, 250 and 500 passes by walking. A pass was a one-way walk, at a natural gait, along the length of the plot. People weighed 60–85 kg and wore lug-soled boots. Notably, shoe type and weight of the trampling person have been shown to exert only very little (Cole 1997) or no influence (Whittaker 1978; Andrés-Abellán *et al.* 2006) on vegetation.

Vegetation surveys took place immediately prior to disturbance, 2–4 weeks post-disturbance – this is because plant death often takes several days to weeks following trampling (Cole & Bayfield 1993) – and again 1-year post-disturbance. Percentage cover for each vascular plant species per plot was visually estimated. Total vegetation cover (excluding litter and dead plant material) was also estimated. For this paper, we excluded woody plants with a size higher than 0.5 m and regenerating trees from analysis. The dominant tree and understorey species lists are found in Appendix S1 (Supporting Information).

SITE-SPECIFIC EXPLANATORY VARIABLES

Site characteristics are summarized in Table 1. Climatic conditions at the sites were quantified by three well-established indices: (i) the continentality index C_S (Schrepfer 1925); (ii) the aridity index A_M (De Martonne 1927); and (iii) a classification of seasonality of precipitation (Kottek *et al.* 2006). C_S and A_M range between 0 (oceanic/arid) and 100 (continental/humid); for the seasonality of precipitation we distinguished between summer-dry and fully humid climates. Further details on these indices are presented in Appendix S1.

Table 1. Characterization of the 35 sites used in the disturbance experiment. Presented are the site name, country, ecosystem (forest or grassland), latitude (°), longitude (°), elevation (m a.s.l.), soil type, background anthropogenic disturbance (hemeroby), continentality C_S (%), aridity A_M (%), climate type (s: summer-dry; f: fully humid), and the cover of the tree layer (TL in %; only forest sites). The classification of soil types followed the Soil Atlas of Europe (European Soil Bureau Network 2005). The classes of hemeroby refer to: 1, ahemrobe (not realized); 2, oligohemrobe; 3, mesohemrobe; 4, beta-hemrobe. For further explanations see text, a list of typical species per site is presented in Appendix S1

Number	Site name	Country	Ecosystem	Latitude	Longitude	Elevation	Soil type	Hemeroby	C _S	A _M	Climate type	TL
1	Gumpenstein	Austria	Grassland	47°29' N	14°06' E	710	Cambisol	4	33.4	59.7	f	—
2	Zöbelboden	Austria	Forest	47°50' N	14°26' E	900	Leptosol	2	25.8	81.4	f	85
3	Bayreuth	Germany	Grassland	49°58' N	11°30' E	355	Cambisol	3	28.9	40.0	f	—
4	Göttingen dry grassland	Germany	Grassland	51°31' N	9°57' E	275	Leptosol	3	23.4	34.4	f	—
5	Gimritz	Germany	Grassland	51°35' N	11°50' E	110	Leptosol	3	26.3	25.9	f	—
6	Göttinger Wald	Germany	Forest	51°31' N	10°01' E	410	Leptosol	2	23.4	34.4	f	90
7	Göttingen orchard meadow	Germany	Grassland	51°32' N	10°03' E	285	Pelosol	3	23.4	34.4	f	—
8	Hainich Lindig grassland	Germany	Grassland	51°05' N	10°31' E	340	Luvisol	3	25.3	30.7	f	—
9	Hainich Thiemsburg	Germany	Forest	51°04' N	10°30' E	350	Luvisol	2	25.3	30.7	f	90
10	Hainich Lindig forest	Germany	Forest	51°05' N	10°31' E	350	Luvisol	2	25.3	30.7	f	95
11	Solling grassland	Germany	Grassland	51°46' N	9°33' E	460	Cambisol	3	22.6	60.8	f	—
12	Solling forest 1	Germany	Forest	51°45' N	9°34' E	495	Cambisol	2	22.7	60.8	f	90
13	Solling forest 2	Germany	Forest	51°45' N	9°33' E	510	Cambisol	3	22.7	60.8	f	55
14	Crozet grassland	France	Grassland	45°05' N	6°02' E	1700	Leptosol	2	22.0	65.9	f	—
15	Mays grassland	France	Grassland	45°06' N	6°03' E	1950	Leptosol	2	22.0	65.9	f	—
16	Nogent-sur-Vernisson forest	France	Forest	47°50' N	2°45' E	150	Luvisol	2	23.8	35.4	f	75
17	Nogent-sur-Vernisson grassland	France	Grassland	47°50' N	2°45' E	150	Luvisol	4	23.8	35.4	f	—
18	Venelles forest	France	Forest	43°36' N	5°31' E	400	Calcisol	2	29.2	28.1	s	45
19	Venelles grassland	France	Grassland	43°37' N	5°23' E	430	Calcisol	3	29.2	28.1	s	—
20	Hindsby forest 1	Finland	Forest	60°21' N	25°11' E	45	Podzol	2	31.1	45.8	f	60
21	Hindsby forest 2	Finland	Forest	60°20' N	25°11' E	55	Podzol	2	31.1	45.8	f	70
22	Hindsby grassland	Finland	Grassland	60°20' N	25°13' E	20	Cambisol	3	31.1	45.8	f	—
23	Alti a'Mharcaidh	Scotland	Forest	57°07' N	3°51' W	390	Podzol	2	13.0	56.2	f	5
24	Invercauld forest	Scotland	Forest	57°00' N	3°19' W	350	Podzol	3	9.9	50.4	f	10
25	Invercauld grassland	Scotland	Grassland	57°01' N	3°20' W	340	Gleysol	3	9.9	50.4	f	—
26	Wytham	England	Forest	51°55' N	1°21' W	135	Cambisol	3	13.2	35.8	f	80
27	Rejtek	Hungary	Forest	48°03' N	20°33' E	510	Leptosol	2	35.8	38.0	f	85
28	Sikföktut forest 1	Hungary	Forest	47°55' N	20°26' E	330	Luvisol	3	38.5	30.9	f	50
29	Sikföktut forest 2	Hungary	Forest	47°55' N	20°26' E	330	Luvisol	2	38.5	30.9	f	80
30	Monte Rufeno	Italy	Forest	42°49' N	11°54' E	680	Cambisol	2	30.7	44.4	s	45
31	Vadu Lat	Romania	Forest	44°20' N	25°40' E	115	Phaeozem	2	50.4	17.6	f	80
32	Braila Island grassland	Romania	Grassland	45°12' N	27°58' E	3	Fluvisol	2	47.3	19.4	f	—
33	Kindla	Sweden	Forest	59°45' N	14°54' E	317	Podzol	2	31.8	64.9	f	10
34	Bab	Slovakia	Forest	48°18' N	17°53' E	198	Cambisol	2	36.9	26.2	f	70
35	Pezinok	Slovakia	Grassland	48°19' N	17°15' E	265	Cambisol	3	36.7	25.1	f	—

Background levels of human disturbance were estimated following the hemeroby index by Steinhardt *et al.* (1999). Sites were ranked (1–5) with increasing human impact: (1) ahemerobe: no human impact; (2) oligohemerobe: limited removal of wood, pastoralism, deposition of nutrients through air and water; (3) mesohemerobe: clearing and occasional ploughing, clear cut, occasional slight fertilization; (4) beta-euhemerobe: application of fertilizers, lime and pesticides, ditch drainage; (5) alpha-euhemerobe: deep ploughing, drainage, application of pesticides and intensive fertilization (no sites in this study). Furthermore, as additional site-specific variables, country, elevation, total cover of the tree layer (only forest sites), and soil type (classification followed the Soil Atlas of Europe, European Soil Bureau Network 2005) were used.

RESPONSE VARIABLES TO EXPERIMENTAL DISTURBANCE

Vegetation response to experimental disturbance was characterized by resistance and resilience indices describing the ability of the vegetation to withstand disturbance and the recovery process, respectively. These were calculated in two steps: (i) we used an index for disturbance intensity (D_{int}) to characterize the vegetation development under the different treatments within each block at each experimental site, which was (ii) used to determine for each block the resistance and resilience indices.

Disturbance intensity (D_{int})

To characterize the impact of disturbance frequency on vegetation development we used total vegetation cover and individual species cover as the basis for our calculations. It has been shown (e.g. Mucina, Schaminee & Rodwell 2000), that cover-values per plant species reflect their percentage contribution to the entire biomass. We used an index called disturbance intensity (D_{int} , ranges between -1 and 1), adapted from the RNE-index (relative neighbour effect, Markham & Chanway 1996), and calculated according to the following formula:

$$D_{\text{int}} = -1 \times \left(\frac{I_{\text{treatment}} - S_{\text{treatment}}}{\max(I_{\text{treatment}}, S_{\text{treatment}}, S_{\text{control}}, I_{\text{control}})} - \frac{I_{\text{control}} - S_{\text{control}}}{\max(I_{\text{treatment}}, S_{\text{treatment}}, S_{\text{control}}, I_{\text{control}})} \right) \quad \text{eqn 1}$$

The first fraction corresponds to the RNE-index, where $I_{\text{treatment}}$ is the initial vegetation cover before disturbance and $S_{\text{treatment}}$ the surviving cover after treatment. Vegetation cover may change between two time steps because of some unmeasured environmental correlate (i.e. not experimental disturbance). Consequently, a correction factor was used (I_{control} = initial vegetation cover on control plots; S_{control} = surviving cover on control plots) to prevent under- ($I_{\text{control}} < S_{\text{control}}$) or over-estimation ($I_{\text{control}} > S_{\text{control}}$) of the disturbance treatment. Thus, D_{int} characterizes the impact of experimental disturbance irrespective of other biotic and abiotic factors. D_{int} was calculated for each treatment per block (four blocks per site), resulting in values for the 25, 75, 250 and 500 intensity treatments. This value was multiplied by -1 so that it would be negative if vegetation cover decreased following disturbance.

In addition, to provide individual species responses we also calculated D_{int} , and subsequently resistance or resilience, for all species present on at least 10 of the 20 plots, and at least three controls, per site. Individual focal species D_{int} was only calculated for a block when the focal species also occurred on the corresponding control plot.

Indices for resistance and resilience

For each block at each site an index of resistance and of resilience was calculated by using the D_{int} -values calculated as above. First, we calculated the area between the lines connecting D_{int} at the different disturbance intensities and the horizontal base-line at a y -axis value of zero (indicates no influence of disturbance) (Fig. 1). This corresponded to the change initiated by disturbance. Secondly, this observed change was expressed as the proportion of the potential maximal change (the total area below the base-line) (Fig. 1). This proportional change indicates vegetation or species resistance if based on D_{int} -values 14-day post-disturbance and resilience if D_{int} -values 1-year post-disturbance were used. Negative values of D_{int} imply a loss of vegetation cover and positive values an increase.

STATISTICAL ANALYSES

Experimental disturbance and D_{int}

To check whether the experimental disturbance treatments altered vegetation irrespective of other biotic and abiotic factors, a regression between D_{int} and disturbance frequency (number of passes) was performed per site to see whether it differed from a null model meaning zero effect of trampling. To account for the nested design used in our study, these regressions were calculated using linear mixed-effect models with sites, and block nested within site, as random effects for total vegetation cover and single species, respectively. As we may assume either a linear or an exponential relationship between D_{int} and increasing disturbance, these regressions were calculated for untransformed and log-transformed trampling intensity values. When no significant effect of trampling was

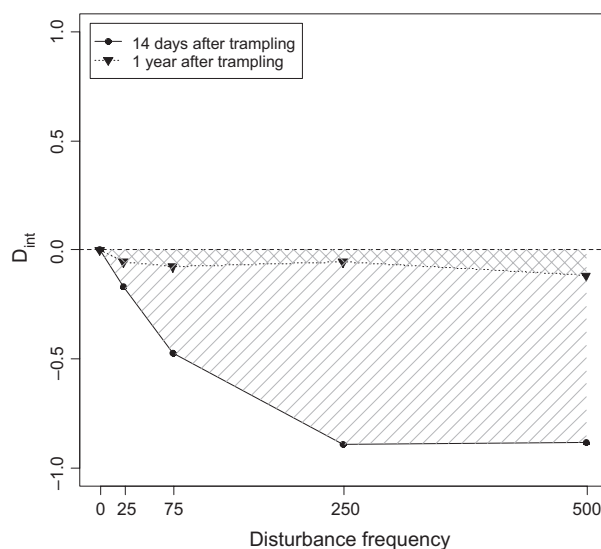


Fig. 1. Visualization of the calculation of the resistance and resilience indices using data from a single grassland site as an example. The example shown is the D_{int} -values of block 2 of the grassland site 'Gimritz' (Number 5 in Table 1) against disturbance frequency (number of passes). D_{int} characterizes the impact of experimental disturbance irrespective of other biotic and abiotic factors and ranges between -1 and 1 . Resistance is calculated as the proportional area between the solid and the dashed line (area indicated by diagonal lines), resilience as the proportional area between the dotted and the dashed line (area indicated by cross-hatching). For further explanations see text.

found, we replaced the D_{int} -values for all trampling intensities by 0. This was performed for D_{int} 14 days after trampling and D_{int} 1 year after trampling.

Relating vegetation resistance and resilience to environmental heterogeneity

Resistance and resilience were fitted as the dependent variable in separate linear mixed-effect models with the categorical variable 'site' as a random effect. Explanatory variables were: ecosystem type (forest or grassland), elevation, soil type, hemeroby, continentality, aridity, seasonality of precipitation, country, tree cover and all two-way interactions. Prior to analysis with mixed models, all numerical explanatory variables were normalized by scaling them between 0 and 1, and checked for possible inter-correlations. Such standardization is required to make the explanatory variables that were measured on different scales comparable. Using a correlation threshold of $r^2 > 0.3$, we found that ecosystem type and tree cover were highly correlated ($r^2 = 0.64$) and consequently removed ecosystem type from the analyses.

Relating vegetation resistance and resilience to plant functional traits

We used another mixed model to detect which functional traits were correlated to vegetation resistance and resilience. Traits were selected that were predicted to be sensitive to disturbance based on literature and author expertise. For the analysed species we extracted trait attributes from the data bases BiolFlor (Klotz, Kühn & Durka 2002), CLOPLA (Klimešová & de Bello 2009) and LEDA (Kleyer *et al.* 2008). All species identified as reacting to experimental disturbance (see above) were assigned to the plant traits maximal canopy height, leaf dry matter content (LDMC), specific leaf area (SLA), leaf size (LS), leaf anatomy, leaf distribution along the stem (LD), type of reproduction, age at first flowering, plant life span, lateral spread and plant growth form (details presented in Appendix S1). Again, correlated traits ($r^2 > 0.3$) were removed prior to analyses. Correlation was detected between lateral spread and reproduction by seeds ($r^2 = 0.49$), and scleromorphic and mesomorphic leaf anatomy ($r^2 = 0.41$); in both cases the latter trait was removed.

Linear mixed-effect models were run with resistance or resilience as dependent variables and uncorrelated plant traits as explanatory variables. Block nested within site was fitted as a random effect. The within-block variance was calculated on all disturbance-sensitive species occurring within each block and encompasses differences among species within a block.

All statistical analyses were performed with R 2.10.1 (R Development Core Team 2009), linear mixed-effect models were run using the package nlme. Maximal models were simplified via backward selection of the least significant variables until the final minimal adequate model contained significant terms only (P -value < 0.05) and a minimal Akaike Information Criterion (AIC) was obtained (Crawley 2007).

Results

RELATING VEGETATION RESISTANCE AND RESILIENCE TO ENVIRONMENTAL HETEROGENEITY

When relating site-specific disturbance indices (presented in Appendix S2) to environmental factors, vegetation resistance

Table 2. Summary statistics of the linear mixed-effect models for resistance and resilience. The table includes estimates, standard errors (SE), degrees of freedom (d.f.), t - and corresponding P -values for all significant environmental variables. Both models were based on 135 observations and the random factor site

	Estimate	SE	d.f.	t -value	P -value
Resistance					
Intercept	0.44	0.06	100	7.33	0.000
Elevation	0.39	0.16	32	2.38	0.023
Hemeroby	0.30	0.11	32	2.65	0.013
Resilience					
Intercept	1.12	0.07	100	16.60	0.000
Cover of the tree layer	-0.13	0.05	31	-2.40	0.023
Aridity	-0.36	0.14	31	-2.60	0.014
Seasonality of precipitation (summer-dry)	-0.24	0.07	31	-3.19	0.003

to disturbance was predicted by hemeroby and elevation (Table 2). Vegetation with greatest resistance was located at higher elevations (Fig. 2a). Resistance was also intensively influenced by human activities as indicated by hemeroby index: oligohemerobe sites had lower resistance than mesohemerobe and euhemerobe sites (Fig. 2b). Grassland sites, in general, showed higher levels of anthropogenic background disturbance in comparison to forest sites (Table 1).

Vegetation resilience to disturbance was predicted by seasonality of precipitation, aridity and hemeroby (Table 2). With respect to climate influences, we found that more humid sites had a higher resilience in comparison to arid sites (Fig. 2c), and sites in fully humid climates were more resilient to disturbance than sites in summer-dry climate (Fig. 2d). A negative relationship between tree cover and lower resilience (Fig. 2e) revealed that grassland sites were more resilient in comparison to forests.

RELATING VEGETATION RESISTANCE AND RESILIENCE TO PLANT FUNCTIONAL TRAITS

Vegetation resistance was predicted by two plant functional traits: leaf size (LS) and leaf distribution (LD) along the stem (Table 3). Resistance was negatively related with leaf size, meaning that plants with higher resistance tended to have smaller leaves (Fig. 3a). Typically, resistant plant species had a rosette life-form: species forming rosettes were more resistant than semi-rosette plants, which were, in turn, more resistant than species with a regular stem leaf distribution (Fig. 3b).

Vegetation resilience to disturbance was predicted by leaf dry matter content (LDMC), specific leaf area (SLA) and scleromorphic leaf anatomy (Table 3). Resilience was negatively correlated to LDMC, thus, plants with higher tissue density were less resilient to disturbance in comparison to those with more fleshy leaves (Fig. 3c). A similar negative pattern was detected between resilience and scleromorphic leaf anatomy. Plants with scleromorphic leaves were less resilient to disturbance than non-scleromorphic plant species (Fig. 3e).

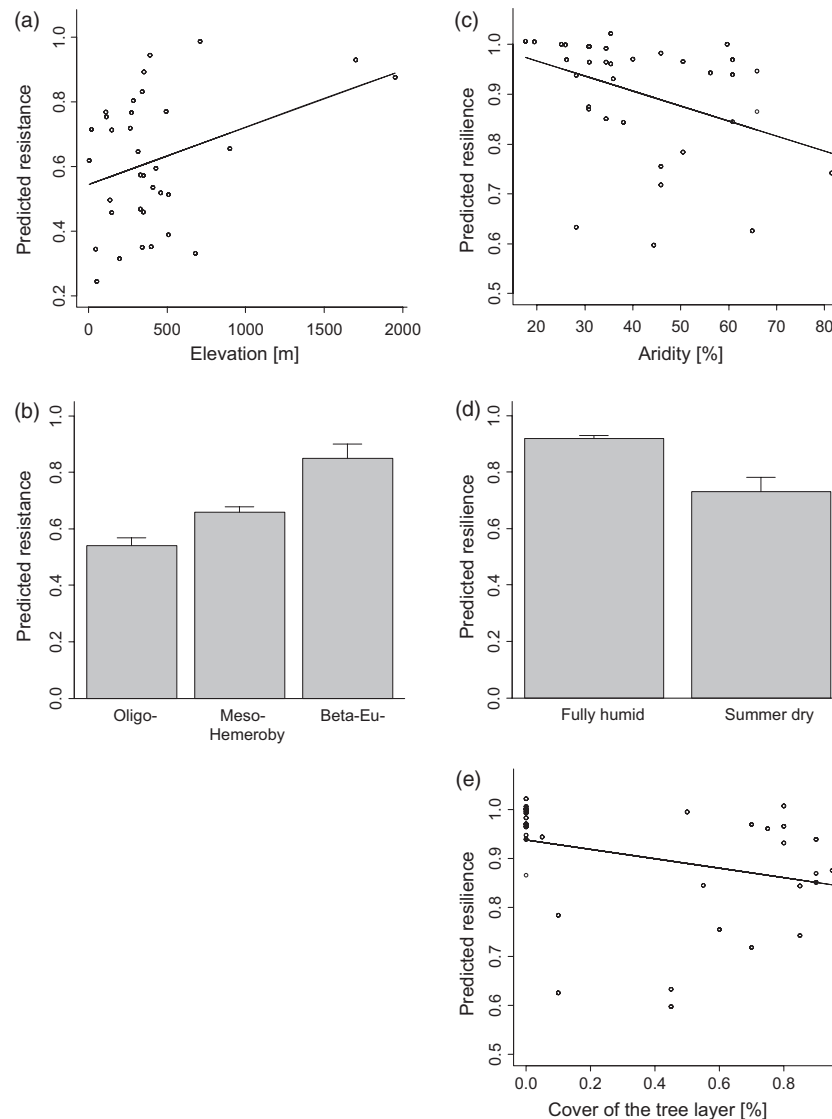


Fig. 2. Predicted resistance (a, b) and resilience (c–e) vs. relevant environmental variables. The predictions were obtained from the linear mixed-effect models presented in Table 2. For numerical variables (a, c, and e) regression lines are shown, for ordinal scaled (b) and factorial variables (d) per-category means and standard errors are presented. All regression lines (a, c, and e numeric data; b ordinal scaled data) were significant, the groups presented in d differed significantly (compare Table 2).

Increasing SLA led to a statistically slight increase in resilience (Table 3), indicating that higher potential growth rates may have some role in increasing vegetation resilience to disturbance (Fig. 3d).

Discussion

This study clearly demonstrates that following experimental disturbance different environmental factors influence the resistance or resilience of vegetation communities and single species. Furthermore, resistance and resilience are related to various functional traits allowing deeper insights into the processes of vegetation development following disturbance events.

Within this study, we analysed vegetation responses following human trampling mainly affecting above-ground plant tissues. Our results produced patterns comparable to those described by Diaz *et al.* (2007) for disturbance by grazing.

Both disturbance by trampling and grazing (Diaz *et al.* 2007) will favour short or prostrate plants, and plants with rosettes. Moreover, neither grazing nor trampling had a consistent effect on growth form, and trait responses to disturbance were modified by climatic and historical context. Grazing and human trampling both principally damage above-ground plant parts. The implication is that the vegetation responses to experimental disturbance in this paper are likely to be consistent with other disturbances damaging above-ground tissues.

RELATING VEGETATION RESISTANCE TO ENVIRONMENTAL HETEROGENEITY AND PLANT FUNCTIONAL TRAITS

The results of the presented study support our first hypothesis that ecosystems with higher background anthropogenic disturbance (such as grasslands) are more resistant to disturbance

Table 3. Summary statistics of the linear mixed-effect models relating resistance and resilience to functional traits. The table includes estimates, standard errors (SE), degrees of freedom (d.f.), *t*- and corresponding *P*-values for all significant traits. Following our selection procedure to detect species reacting on disturbance we found in total 130 species reacting; as these may occur at several sites in total 223 populations were considered for further analyses. The models were based on 829 observations for resistance and resilience, and the random factors blocks nested within sites. LS, leaf size; LDMC, leaf dry matter content; LD, leaf distribution along the stem; SLA, specific leaf area

	Estimate	SE	d.f.	<i>t</i> -value	<i>P</i> -value
Resistance					
LS	-0.48	0.23	686	-2.08	0.038
LD (rosette)	-0.08	0.06	686	-1.40	0.162
LD (semi-rosette)	-0.17	0.03	686	-5.21	0.000
LD (regular)	-0.31	0.03	686	-9.44	0.000
Resilience					
Intercept	0.20	0.06	688	3.23	0.001
LDMC	-0.20	0.08	688	-2.65	0.008
SLA	-0.21	0.10	688	-2.07	0.039
Scleromorph leaf anatomy	-0.16	0.05	688	-3.25	0.001

events than less frequently affected or less managed ecosystems such as forests. For human trampling Hill & Pickering (2009) compared 65 studies from different vegetation types (most of these without human land-use) according to their resistance and found the following overall pattern (sorted by decreasing resistance), which accords with our results: sand-dune grasslands > grasslands > sand-dune heaths > forest understorey > heaths \approx herb-fields. This vegetation sequence can be explained by the different species assemblages being a product of species-specific responses (e.g. adaptation) to local environmental conditions, land-use history, and management. Sand-dune grasslands are very dynamic ecosystems with a high amount of biotic (e.g. animals) and abiotic (e.g. storms) disturbances. In contrast, grasslands, forests and heath lands are all regularly affected by human land-use (like grazing, mowing or logging), but disturbance frequency and intensity are generally much higher in grasslands compared to forests. Thus, when analysing assemblages composed of species with pre-adaptations that allow persistence it might be useful to categorize them according to human impact (degrees of hemeroby, Hill, Roy & Thompson 2002), instead of an assignment to broad ecosystem types only.

Focussing on our second hypothesis that resistance is modified by climate and local site factors, no influence of aridity, soil type, cover of the tree layer and continentality on resistance was detected. There was a suggestion of a positive relationship between resistance and elevation (higher at higher elevation), in agreement with our hypothesis and Gomez-Garcia, Azorin & Aguirre (2009). It should be acknowledged, however, that the relationship in our study was dependent on only two sites at the highest elevations; more data at this end of the elevation gradient would be needed to support unequivocally the idea that resistance to disturbance is greater at higher altitudes.

A functional-trait approach was applied to get insights into the processes of vegetation adaptations to resist single disturbance events. The observed relationship between morphological traits and resistance supported our third hypothesis to some extent, namely, that slow-growing plants with below-ground buds have a high resistance. For example, we found that plants with smaller leaves were resistant to disturbance, a result in agreement with Arnesen (1999). However, in contrast to the studies by Roovers, Baeten & Hermy (2004) and Liddle (1975) we did not find that plant life-form explained differences in resistance. These authors characterized juvenile phanerophytes and chamaephytes as sensitive to disturbance because their buds are distant from the ground and, therefore, directly exposed to the applied disturbance treatment. In this paper, we found no simple effect of plant life-form on vegetation resistance (but we did not measure tree regeneration). Instead we found that among the hemicryptophytes, therophytes and chamaephytes the differential response to disturbance was between plants with rosettes or regular stem leaf distributions.

RELATING VEGETATION RESILIENCE TO ENVIRONMENTAL HETEROGENEITY AND PLANT FUNCTIONAL TRAITS

The ability of vegetation to redevelop when damaged, i.e. its resilience, is crucially important in predicting responses to disturbance or other environmental change. Contradicting our first hypothesis, we did not find differences in resilience between ecosystems with different background anthropogenic disturbances. In addition, the second hypothesis that resilience depends on climate and local site factors was only partly supported. In this study, ecosystems receiving high irradiation were more resilient to experimental disturbance; moreover, aridity and seasonality of precipitation were negatively connected to vegetation resilience. All these factors are closely related to plant growth rates (Bradford *et al.* 2006): enhanced growth rates are only possible if a suitable amount of water and light is available. In more arid regions a severe lack of available water limits the growth and development of plants (Reich *et al.* 1999; Knapp & Smith 2001), a pattern which is more pronounced if the climate is characterized as summer drought (dryness during the main vegetation period as in the Mediterranean). Generally, potential plant growth will be highest at high irradiation and balanced water supply during the main vegetation period (Reich *et al.* 1999). Such patterns are even clearer when looking at the functional-trait composition of the most resilient plants: these had low LDMCs, high SLA and less often a scleromorphic leaf anatomy (Cornelissen *et al.* 2003). All these trait responses can be related to plant potential growth rates: potential plant growth rates are known to be highest at low tissue densities (low LDMC but high SLA), which are additionally negatively related to scleromorphic leaf anatomy. Species with high tissue densities (like sclerophyllous plants) invest more into dense or thick leaf structure components like lignified cell walls, thick cuticles or other structures stabilizing the leaves (Andrés-Abellán *et al.* 2006). Thus, higher tissue densities are associated with greater

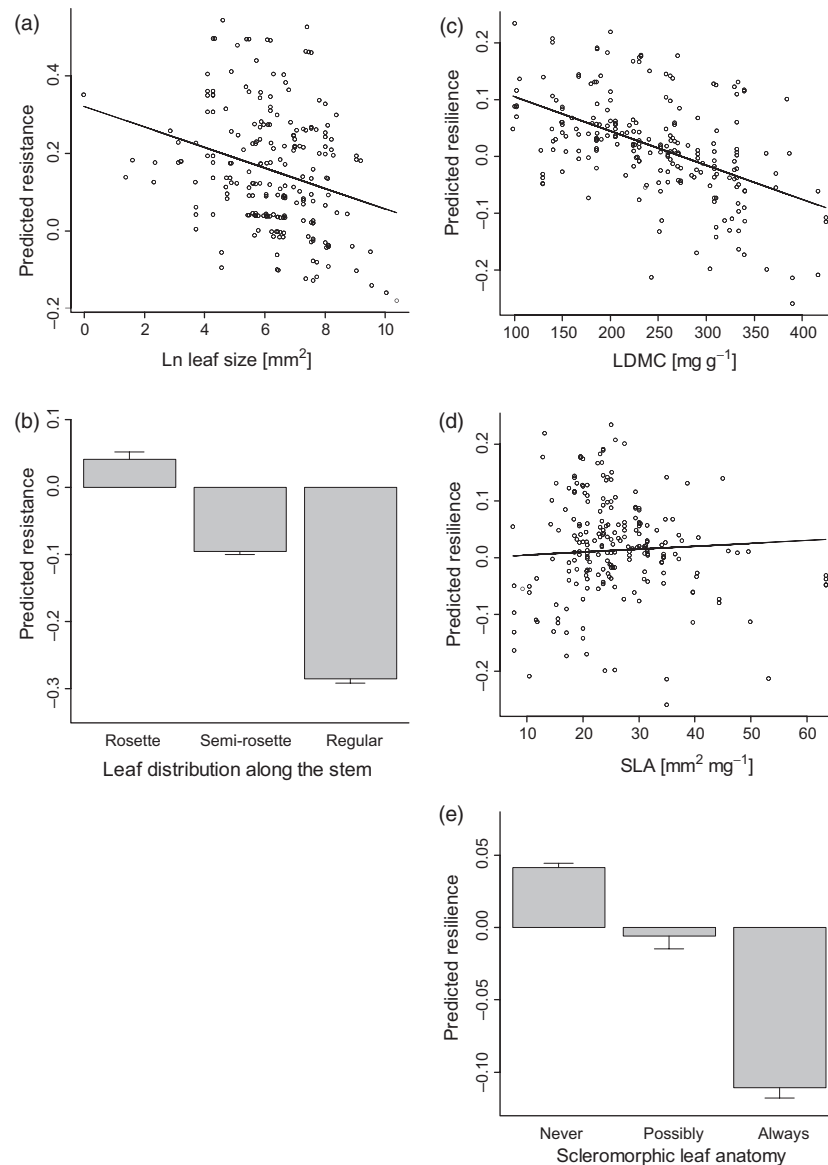


Fig. 3. Predicted resistance (a–b) and resilience (c–e) vs. responsive functional traits. The predictions were obtained from the linear mixed-effect models presented in Table 2. For numerical variables (a, c, d) regression lines are shown, for the ordinal scaled (e) and factorial variables (b) per-category means and standard errors are presented. All regression lines were significant, the groups presented in b differed significantly (compare Table 3).

allocation of biomass to structural than to metabolic components, enhancing the leaf strength and durability, but also resulting in greater leaf internal shading (Lloyd *et al.* 1992; Poorter & De Jong 1999; Reich *et al.* 1999). This trade-off between tissue density and potential growth rates clearly refers to a trade-off between plant resistance and resilience: those plants perfectly adapted by their leaf characteristics to redevelop following disturbance are those with low potentials to withstand the direct impact of disturbance.

Conclusions

Based on vegetation responses to human trampling, our study clearly revealed that resistance and resilience, the two components of ecosystem stability, are strongly affected by environ-

mental factors. For resistance, our results highlight background anthropogenic disturbance leading to species adaptations that potentially increase the ability to withstand disturbances (e.g. small leaves, rosettes). For resilience, environmental factors and functional traits related to potential growth rates were found to be the most important (e.g. aridity, continentality, LDMC or SLA).

The implications of our findings for the management of recreational activities are that sustainable numbers of visitors to natural ecosystems will depend on vegetation, land-use history and climate. Resistance primarily depends on the functional composition of the predominant species, which is more strongly affected by land-use history than climate, whereas the resilience of an ecosystem is largely dependent on plant growth and is therefore directly connected to climate (e.g. temperature

and moisture). This paper's findings strongly argue for the inclusion of land-use history into the planning of visitor management in nature conservation areas. Furthermore, plant community responses to recreational activities may change in future when the vegetation's ability to redevelop following disturbance will be altered by climate change. Thus, we should move towards a planning of visitor management that includes physical as well as physiological responses.

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Appendix S1. Further information on materials and methods.

Appendix S2. Supporting results.

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