RESEARCH ARTICLE

Restoration of Heterogeneous Disturbance Regimes for the Preservation of Endangered Species

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ABSTRACT

Disturbance is a natural component of ecosystems. All species, including threatened and endangered species, evolved in the presence of, and are adapted to natural disturbance regimes that vary in the kind, frequency, severity, and duration of disturbance. We investigated the relationship between the level of visible soil disturbance and the density of four endangered plant species on U.S. Army training lands in the German state of Bavaria. Two species, gray hairgrass (*Corynephorus canescens*) and mudwort (*Limosella aquatica*), showed marked affinity for or dependency on high levels of recent soil disturbance. The density of fringed gentian (*Gentianella ciliata*) and shepherd's cress (*Teesdalia nudicaulis*) declined with recent disturbance, but appeared to favor older disturbance which could not be quantified by the methods employed in this study. The study illustrates the need to restore and maintain disturbance regimes that are heterogeneous in terms of the intensity of and time since disturbance. Such a restoration strategy has the potential to favor plant species along the entire spectrum of ecological succession, thereby maximizing plant biodiversity and ecosystem stability.

Keywords: fringed gentian, gray hairgrass, heterogeneous disturbance hypothesis, mudwort, shepherd's cress

Ecosystems and the species that inhabit them typically evolve in the presence of quasi-stable disturbance regimes which are characterized by general patterns of perturbation, including the types of disturbance and their frequency, intensity, size, periodicity, and/or duration. Significant alteration of the disturbance regimes has the potential to negatively affect native biodiversity. The restoration of biodiversity is a common goal of restoration ecologists around the globe. However, the process is often more complicated than it initially appears, and may well involve the restoration of the disturbance regime in addition to the reintroduction of native species (Jentsch 2007). This can be particularly important for threatened and endangered species that are dependent on a particular disturbance regime to create and maintain conditions necessary for survival.

Ecological Restoration Vol. 32, No. 2, 2014
ISSN 1522-4740 E-ISSN 1543-4079

The grasslands of northern Europe lie within what would be mostly forest in the absence of disturbance. Prior to recent anthropogenic alteration of disturbance regimes, the grasslands were maintained for approximately 1.8 million years by wild ungulate herbivores (Pärtel et al. 2005). During the last millennium, wild ungulates have been largely replaced by domestic herbivores. More recently, the abandonment of traditional grazing practices and increased use of agricultural fertilization have resulted in a dramatic decrease in the spatial extent and biodiversity of the grasslands (Jentsch and Beyschlag 2003, Butaye et al. 2005, Isselstein et al. 2005).

During the Cold War, military training areas represented some of the largest tracts of grassland in northern Europe. Disturbance created by military training maneuvers provided an effective surrogate for the disturbance under which the grasslands evolved. When the European Commission issued Directive 92/43/EEC (European Economic Community 1992) requiring all European Union nations to designate a certain percentage of their landmass as 'special areas of conservation' in the NATURA 2000 network, many nations recognized the ecological value of their military training areas. As a result, they nominated large tracts of their training lands. For example, Denmark nominated 45% of its military training landmass, while the Netherlands included 50%, and Belgium 70% (Gazenbeek 2005). In Germany, military training areas provide suitable habitat for a greater density of Red List (the European counterpart of U.S. 'threatened and endangered') animal species than provided by most other 'special areas of conservation' (Warren et al. 2007).

In the post-Cold War era, numerous military training areas in Europe have been abandoned or have experienced a significantly diminished frequency and intensity of military-related disturbance. Many, with extensive and diverse grasslands, have experienced encroachment of woody species and concomitant reductions in the populations of species that depend on grasslands maintained by disturbance (IUCN 1996, Chojnacka et al. 2010, Tschöpe et al. 2011).

Our hypothesis, based on years of personal observation on the U.S. Army training areas in Germany, was that numerous Red List plant species were favored by the disturbance regime related to military training activity. The objective of this effort was to test the hypothesis and determine the degree to which it was valid. Assuming the hypothesis was supported by the research data, the information will assist restoration ecologists in identifying and quantifying an appropriate disturbance regime to maintain these threatened and endangered plant species.

Methods

Study Species

We evaluated four Red List plant species occurring on U.S. Army training areas in the German state of Bavaria. Gray hairgrass (*Corynephorus canescens*) is a densely tufted, glaucous perennial grass that grows to 30 cm. It is listed as endangered on the Bavarian Red List. It occurs most frequently on sandy, acidic grasslands with loose sand (Oberdorfer 1990, Rothmaler 1994). Mudwort (*Limosella aquatica*) is a small annual forb that prefers loamy or clayey soils and occurs most commonly in moist areas along the margins of ephemeral water puddles (Rothmaler 1994, Rosenbauer 1996). It can grow to a height of 12 cm and is listed as endangered on the Bavarian Red List. Fringed gentian (*Gentianella ciliata,* syn. *Gentiana ciliata* and *Gentianopsis ciliata*), is a small, late-flowering biennial that is listed as endangered on the German Red List, is on the early warning list for Bavaria, and requires protection under Germany's Federal Nature Protection Act. It grows erect to 25 cm and occurs on dry grasslands with soils similar to mudwort, but without the additional moisture (Rothmaler 1994, Rosenbauer 1996). Shepherd's cress (*Teesdalia nudicaulis*) is a small annual forb that is listed as endangered on the Bavarian Red List. It occurs on sandy, acidic grasslands (Schulze-Motel 1986, Oberdorfer 1990).

Study Area

We sampled plant populations at four active U.S. Army training facilities in the state of Bavaria: Grafenwöhr Training Area (GTA); Hohenfels Training Area (HTA); Freihölser Forst Local Training Area (FFTA); and Klosterforst Training Area (KTA). GTA is approximately 23,000 ha in size. It was first used by the Royal Bavarian Army in 1910 and has been used continuously since that time, with control ceded to the U.S. Army at the end of World War II (Burkhardt 1994). The training area is located between the towns of Vilseck and Grafenwöhr, about 88 km northeast of Nürnberg. The western third of the training area is characterized by calcareous soils; the eastern part is composed mainly of sandy soils. It is situated in a low-lying area with numerous streams, small lakes and swampy areas. Average annual precipitation is approximately 630 mm.

HTA is approximately 16,000 ha in size. It has been used almost continuously since it was established in 1938 by the German Army (Burkhardt 1994). It is located approximately 84 km southeast of Nürnberg. The training area is characterized by hilly terrain with softly rounded rock formations, karst topography, mixed coniferous and deciduous forest, and dry valleys. The soils in the training area are mostly clay loams derived from weathered limestone or dolomite. Dolomitic sands are also present. Average precipitation is between 650 mm and 700 mm per year. Drainage is predominantly internal, with much of the water entering the karst system.

FFTA is located approximately 35 km northeast of HTA and 5 km southeast of the town of Amberg. It comprises approximately 138 ha. Due to intensive training activities during the 1960's, large areas were converted into barren sand. While large sandy meadows and open sandy soil can still be found, the open character is currently threatened by shrub invasion and increasing crown density of reforested areas.

KTA comprises approximately 1,088 ha and is situated northeast of the town of Kitzingen. It lies in a large Pleistocene sand dune area. Mixed layers of sand and gravel deposits from the nearby Main River and former sand dunes characterize the subsoil. The area has been used for military training since before World War I, first by the German Army and, since World War II, by the U.S. Army. Prior to military usage, the area was mostly forested with a mixture of hardwood and coniferous forest. Approximately 100 ha were cleared for military maneuvers and have remained open since that time.

Data Collection

Field methods varied based on the species of interest. Gray hairgrass was found and surveyed at GTA, KTA and FFTA. We used a plot size of 5 m × 5 m, or 25 m². One hundred plots were established; 29 at GTA, 21 at KTA, and 50 at FFTA in areas where the species was found. Because the objective was to ascertain the relationship, if any, between disturbance and species abundance, the plots were equally distributed among areas representing 5 levels of physical ground disturbance (i.e. 0–20, 21–40, 41–60, 61–80, and > 81%). A conservative definition of disturbance was used, labeling as disturbed only the portion of the plots where recent, definitive ground disturbance was evident (e.g., visible vehicle tracks, damaged plants, displaced soil, etc.); the mere absence of vegetation was considered insufficient to definitively indicate recent disturbance. Six transects were established at 1m intervals, and perpendicular to one end of each plot. At 1 m intervals along each transect, the presence or absence of disturbance was recorded (36 points per plot) as a quantitative estimate of the percent disturbance in the plot. All individuals of gray hairgrass were counted by plot.

Circular plots with a radius of 3 m and an area of 28.3 m² were used to measure fringed gentian, mudwort, and shepherd's cress. Fringed gentian and mudwort were surveyed in 50 plots each at GTA and in an additional 50 plots each at HTA. For shepherd's cress, fifty survey plots were established in suitable habitat at GTA; 50 additional plots were established at FFTA. Plots for all species were distributed evenly among areas representing the same five levels of relatively uniform ground disturbance as used for gray hairgrass.

Statistics

To maximize comparability with existing and future studies, all count data were converted to density (numbers per m²) prior to statistical analyses. Disturbance levels in each plot were converted to one of the five disturbance level categories. Analyses of variance were computed for each species using the SYSTAT 13 analytical software (SYSTAT Software, Inc., Chicago, IL). The analyses tested the effects of the level of disturbance and study site on the density of the respective species. Statistical outliers were removed when encountered to prevent effects on the results and conclusions. When the analyses of variance revealed significant differences between treatments or sites, post-hoc separation of means were computed using the Fisher's LSD method with a probability level of 0.05.

Table 1. The degrees of freedom (df), mean squares, F-ratios and *p*-values associated with the analyses of variance on the differences between study sites and levels of disturbance for each of the four species evaluated in this study.

	df	Mean square	F	*p*
Gray hairgrass				
Study sites	2	33.89	2.27	0.110
Levels of disturbance	4	65.98	4.41	0.003
Interaction	8	20.28	1.36	0.227
Error	82	14.93		
Mudwort				
Study sites	1	0.02	0.03	0.870
Levels of disturbance	4	0.87	17.29	0.000
Interaction	4	0.17	0.28	0.895
Error	143	0.63		
Fringed gentian				
Study sites	1	0.01	1.93	0.168
Levels of disturbance	4	0.03	4.97	0.001
Interaction	4	0.01	1.26	0.293
Error	93	0.01		
Shepherd's cress				
Study sites	1	23.16	2.23	0.139
Levels of disturbance	4	28.63	2.76	0.033
Interaction	4	2.07	2.03	0.097
Error	84	10.37		

Results

There were no statistical differences in the density of any of the examined species that could be attributed to the study sites; the percentage of the soil surface showing visible signs of recent disturbance significantly affected all species (Table 1).

Across all 3 locations where it was present, the density of gray hairgrass did not vary significantly between the two lower levels of disturbance, i.e. 0–20% and 21–40%, but the density at these two levels of disturbance was statistically less than the density in the two highest levels of disturbance, i.e. 61–80% and > 81% (Figure 1). Density in the mid-range disturbance category (41–60%) was intermediate between the lower and higher disturbance categories, and not statistically different from them.

Mudwort followed a similar trend to gray hairgrass, increasing in density at greater levels of disturbance (Figure 2). The density of this forb was greatest at >81% surface disturbance, and significantly less or absent at lower levels of disturbance. Although the density of mudwort trended upward as disturbance increased among the lower disturbance levels, the differences were not statistically significant until reaching the greatest disturbance level.

The density of fringed gentian did not vary significantly among disturbance levels below 61% (Figure 3). It declined precipitously thereafter, and was absent when disturbance exceeded 80%. The density of shepherd's cress trended down as the level of disturbance increased (Figure 4). The density was significantly lower at > 81% disturbance than at 0–20% and 41–60% disturbance. Because of high variability within disturbance levels, no other statistical differences in plant density by disturbance level were evident.

Discussion

The four plant species sampled in this study are considered to be threatened or endangered (Red List) under German and/or European Union guidelines, and all have been reported as occurring on disturbed sites. Our data show that gray hairgrass and mudwort tend to be early successional species that colonize sites that show clear visible evidence of physical disturbance. Fringed gentian and

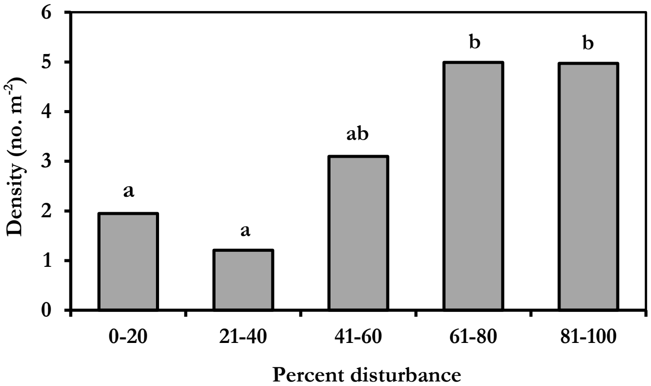

Figure 1. The density of gray hairgrass in plots representing different levels of visible surface disturbance at Grafenwöhr Training Area, Klosterforst Training Area, and Freihölser Forst Training Area, Germany. Bars with different letters differ significantly ($p < 0.05$).

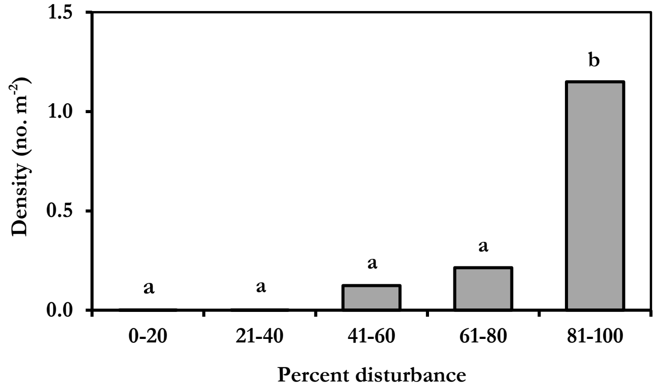

Figure 2. The density of mudwort in plots representing different levels of visible surface disturbance at Grafenwöhr Training Area and Hohenfels Training Area, Germany. Bars with different letters differ significantly ($p < 0.05$).

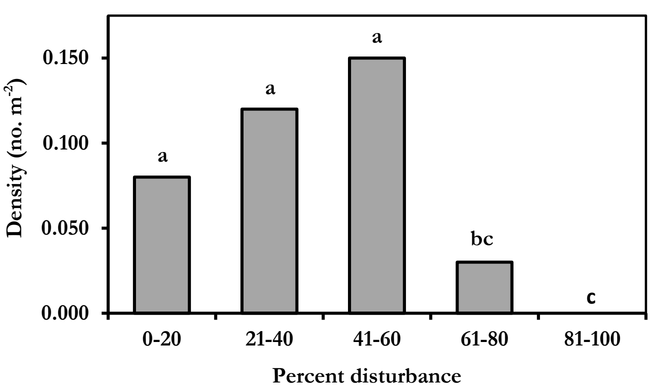

Figure 3. The density of fringed gentian in plots representing different levels of visible surface soil disturbance at Grafenwöhr Training Area and Hohenfels Training Area, Germany. Bars with different letters differ significantly ($p < 0.05$).

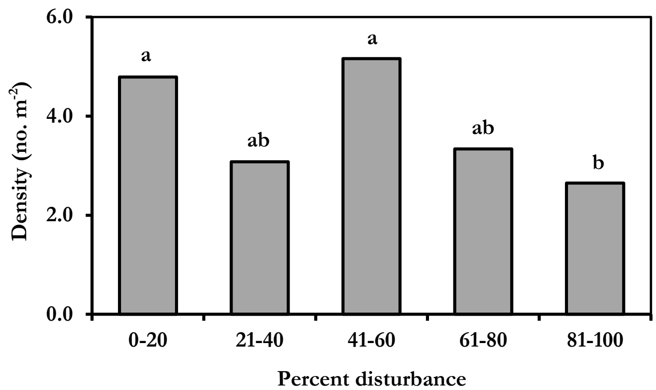

Figure 4. The density of shepherd's cress in plots representing different levels of visible surface soil disturbance at Grafenwöhr Training Area and Freihölser Forst Training Area, Germany. Bars with different letters differ significantly ($p < 0.05$).

shepherd's cress occur somewhat later in successional progression, after clear evidence of physical disturbance may no longer be readily apparent. Examples of disturbance-dependent threatened and endangered amphibians and insects have also been documented on military training areas (Warren and Büttner 2008a, b). The situation presents somewhat of a quandary for land managers who are expected to manage for biodiversity and for the preservation of threatened and endangered species, as such species may occur variously along a successional gradient. It may be considered illogical or even impossible to manage simultaneously for species along an entire successional gradient. And, indeed, it would likely be impossible on homogenously managed landscapes.

Gray hairgrass exhibited affinity for physical soil disturbance, occurring significantly more frequently where disturbance was plainly evident, and being significantly less frequent where disturbance was less. Gray hairgrass is known as a pioneer species, colonizing recently disturbed ground (Tschöpe and Tielbörger 2010, Ödman et al. 2011). It benefits, in terms of seedling emergence, establishment, and fruiting success, from physical soil disturbance (Jentsch et al. 2002, Eichberg et al. 2007, Jentsch et al. 2009) and sand deposition (Hasse and Daniëls 2006). It is commonly reported on dry, nutrient-poor grasslands derived from coastal (Łabuz and Grunewald 2007, Lomba et al. 2008) and inland (Ujházy et al. 2011) sand dunes. Such grasslands generally support a sparse sward of vascular plants and numerous lichens (Jentsch and Beyschlag 2003, Hasse and Daniëls 2006), and progress toward woody vegetation where disturbance is insignificant or absent for long periods (Jentsch and Beyschlag 2003). Various forms of physical disturbance help maintain conditions favorable for gray hairgrass, including excavation by ants and mammals (Jentsch et al. 2002), burial by wind-blown sand (Marshall 1965, Forey et al. 2008), surface mining (Wiegleb and Felinks 2001, Felinks and Wiegand 2008, Řehouková and Prach 2008), trampling by domesticated and wild ungulates (Kooijman and de Haan 1995, Daniëls et al. 2008, Tschöpe et al. 2011) and military training maneuvers (Jentsch et al. 2009, Chojnacka et al. 2010).

Mudwort also exhibited clear signs of disturbance-dependence, being essentially absent at visible disturbance levels less than 81%. This may be due to the fact that most pools and puddles present on the military training areas utilized in this study were caused by vehicle traffic on wet soil. Mudwort is a pioneer species known to occur preferentially in habitats that are regularly and shallowly inundated (Matevski and Kostadinovski 2009, Fischer et al 2010), often on muddy river banks (Csiky and Purger 2008). It is an annual or short-lived perennial that thrives in shallow water for up to a few weeks, and then persists in the mud after water has receded. It was historically known to occur in the ruts of farm carts (Salisbury 1970) and in porcine pastures where the rooting behavior of pigs created small barren areas that collected pools of water (Beinlich and Poschlod 2002). Due largely to the decline of pasturing and other disturbances on seasonally wet, muddy habitat, mudwort has declined markedly (Salisbury 1970) and has reached a state of endangerment in several European nations (Király et al. 2008).

Evidence of dependence on disturbance was less clear with fringed gentian. Because of the conservative field definition of disturbance used in this study, points with a history of disturbance, but which no longer showed irrefutable evidence at the ground level, were not labeled as disturbed. Figure 5 is an example of a fringed gentian plot. It appears obvious that a military battle tank had traversed the area at some point in the past. Given that the spruce species (*Picea abies*) pictured typically produces a single whorl of branches annually, and allowing a few years for seeds to be transported and germinate, it could be estimated that the plot was disturbed at least 10 years previously. Husáková (1996) lists fringed gentian as a ruderal species while Jentsch and Beierkuhnlein (2008) suggest that fringed gentian has low competitive capacity and requires open soil and safe sites for germination. Near the same geographic area, Poschlod et al. (2008) reported that fringed gentian tends to occupy recent grasslands and old field borders. In a long-term study near Göttingen, Germany, Bornkamm (2006) recorded the presence of fringed gentian for the first time some 19 years following the cessation of disturbance on grassland that had been historically grazed. It reached

Figure 5. A typical location at Grafenwöhr Training Area, Germany where fringed gentian was found.

Figure 6. A typical location at Freihölser Forst Training Area, Germany where shepherd's cress was found.

maximum density about 25 years post-disturbance, before disappearing altogether, presumably due to competition. Fringed gentian became a significant component of the flora of fallow land in Poland approximately 10–15 years after agricultural fields had been abandoned (Woch 2011).

Shepherd's cress, like fringed gentian, did not show evidence of dependence on disturbance, given our conservative definition of disturbance. Figure 6 is typical of the shepherd's cress habitat we encountered. Although obviously disturbed at some point in the past, the methodology employed prevented labeling points as being definitively disturbed. Shepherd's cress has been reported on abandoned agricultural land (Valachovič 2012), agricultural set asides (Berger et al. 2003), periodically disturbed gravel bars (Gilvear and Willby 2006), abandoned military training areas (Jentsch et al. 2002), and clandestine graves (Caccianiga et al. 2012).

On militarized landscapes, inherent landscape heterogeneity, coupled with military training doctrine, serves to create highly heterogeneous disturbance patterns (Herl et al. 2005, Warren and Herl 2005). Because of the heterogeneous nature of disturbances occurring on military training areas, they are among the most biodiverse habitats in regions where they occur (Flather et al. 1994, IUCN 1996, Groves, et al. 2000, Warren et al. 2007). In accordance with the heterogeneous disturbance hypothesis (Warren et al. 2007), others have likewise concluded that heterogeneous disturbance is vital for conserving biodiversity on non-militarized landscapes (e.g., Vandvik et al. 2005, Fuhlendorf et al. 2006, Massada et al. 2009). The challenge, for practitioners of ecological restoration, is to develop and implement land management strategies that create and maintain a heterogeneous landscape composed of a mosaic of patches of varying age and resulting from a variety of different kinds and intensities of disturbance that mimic natural disturbances regimes. Only recently have researchers and land managers begun to advocate deliberate implementation of heterogeneous land disturbing activities as a means of restoring biodiversity following the cessation or disruption of natural disturbance regimes (e.g., Jentsch et al. 2009, Ödman et al. 2012).

Acknowledgements

We express appreciation to Debra Dale, Martin Elyn and Wolfgang Grimm of the Installation Management Command in Heidelberg, Germany for their financial and logistical support for the effort, and to the commanding officers of the 7th Army Training Command and the individual military installations for site access.

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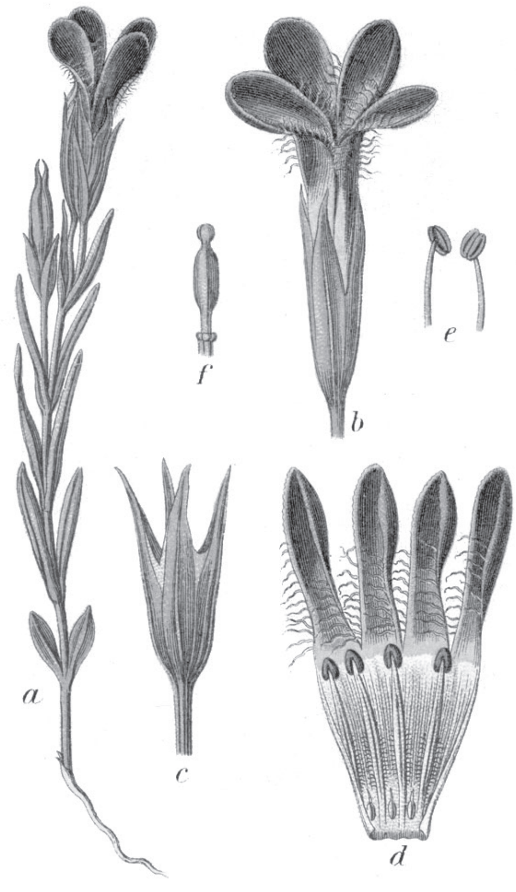

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