Heterogeneity, disturbance and phytodiversity in a human shaped environment: a comparison of semi-natural and agricultural landscapes in Central Europe

by

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Heterogeneous landscape at Grafenwöhr Training Area

I. TABLE OF CONTENTS

SUMMARY

For decades a worldwide decline of biological diversity has been reported. Landscapes are influenced by several kinds of anthropogenic disturbances. Agricultural land use, application of fertilizers and pesticides and the removal of corridors simplify and homogenize a landscape whereas others like road constructions lead to fragmentation. Both kinds lead to a constraint of habitats, reduce living environment and gene pool, hinder gene flow and change the functional characteristics of species. Furthermore, it facilitates the introduction of alien species. On the other hand, disturbances of different temporal and spatial dimensions lead to a more diverse landscape because they prevent competitive exclusion and create niches where species are able to coexist.

This study focuses on the complexity of disturbance regimes and its influence on phytodiversity. It differs from other studies that mostly select one or few disturbance types in including all identifiable disturbances. Data were derived from three study sites in the north of Bavaria and are subject to different land-use intensities. Two landscapes underlie agriculture and forestry, of which one is intensively used and the second one rather moderate and small-scaled. The third dataset was collected on an actively used military training area. The first part of the study deals with the influence of disturbance regimes on phytodiversity, first with the focus on military disturbances, afterwards in comparison with the agricultural landscapes. The second part examines the influence of disturbance regimes on red-listed species, the distribution of neophytes and generalist plant species and the homogenization of the landscape. All analyses were conducted on landscape and local scale.

A decisive role was played by the variety of disturbance types, especially in different temporal and spatial dimensions and not by single kinds of disturbances, which significantly was proven in the military training area with its multiple and undirected disturbance regime. Homogeneous disturbance regimes that typically are found in agricultural landscapes led to a reduced species number. On local scale, the abiotic heterogeneity which originated of recent and historical disturbances superimposed the positive effects of disturbance regimes, whereas dry and nutrient-poor sites showed a negative effect. Due to a low tree density and moderate treatment species numbers were significantly higher in forest in the training area than in the two agricultural landscapes.

Numbers of red-listed species were positively correlated to the total number of species in all three sites. However, the military training area showed a significantly higher abundance within the area in comparison to the agricultural landscapes where rare species were mostly found on marginal strips. Furthermore, numbers of neophytes and generalist species were lower and consequently homogenization.

In conclusion, the military training area is an ideal landscape from a nature conservation point of view. The moderately used agricultural area showed high species numbers and agricultural productivity. However, yield is too low to withstand either abandonment or land-use intensification.

Chapter 1

1 GENERAL INTRODUCTION

1.1 PREFACE

Naturalists and nature lovers like Carl Linnaeus, Alexander von Humboldt, Charles Darwin, and Alfred Russel Wallace were studying the diversity of life for centuries, but the dimension of diversity was realized not until the second half of the twentieth century, when research put its focus on the tropics.

More than 250 years after Linnaeus published the system of binominal nomenclature in *Systema Naturae* (Linnaeus 1758), about 1.25 million to 1.5 million species (May 1988; Mora *et al.* 2011) of the up to 10 million predicted species (McNeely *et al.* 1990; Raven 2001) have been described. Beyond the currently estimated 6.5 million terrestrial species (Mora *et al.* 2011), only 250,000 to 350,000 are plant species (Myers 2001; Kreft & Jetz 2007; Paton *et al.* 2008). According to May (1988) there are roughly twice as many species in the tropical regions as in temperate ones, Joppa *et al.* (2011b) see most of the undiscovered plant species in biodiversity hotspots.

Biological diversity has become a matter of public preoccupation and part of political debates after the 1992 Rio Earth Summit (Magurran 2004). One of the major topics that concerns and divides scientific community is the biodiversity loss. Five publications in the renowned journals Science and Nature display the short period between the awareness of the immense species richness on one side and the species loss on the other side:

Jared M. Diamond asked in 1985: "How many unknown species are yet to be discovered?" (Diamond 1985). May (1988) wondered "How many species are there on earth?". Pimm *et al.* (1995) cared about "The future of biodiversity", Barnosky *et al.* (2011) were afraid, that the "earth's sixth mass extinction has already arrived", and Costello *et al.* (2013) concerned if "we can name earth's species before they go extinct?"

The rate of species loss recorded within the past 300 years for a few groups of organisms is at least several hundred times the rate expected on the basis of the geological records (Dirzo & Raven 2003; Tedesco *et al.* 2014) and is accelerated through the destruction of natural habitats (Ehrlich & Wilson 1991). Many ecologists take this as incentive to unravel the mechanisms responsible for the co-existence of species and the maintenance of biodiversity (Morris & Heidinga 1997; Berendse 2005). The Millennium Ecosystem Assessment took a firm stand in identifying the essential role of ecosystem biodiversity and the need of preservation because it provides provisioning, regulating, supporting, and cultural services (UNEP 2005a; Gaujour *et al.* 2012).

But what exactly is biodiversity and why is it that important for us?

1.2 BIODIVERSITY

1.2.1 What is biodiversity and why is it important?

The term biodiversity or biological diversity has become a winged word and was first introduced by Thomas E. Lovejoy in 1980, when he projected global extinction rates in the Global 2000 Report to the President (Barney 1980). In most studies biodiversity is connected to species richness or number of species (Beierkuhnlein 2001; Balvanera *et al.* 2006; Laliberté *et al.* 2010), and according to Gaston (1998) the "common currency" since it is the simplest index of biodiversity (Francis & Currie 2003). However, it is widely agreed that species richness is just one component of biological diversity (Mönkkönen 1994; Swingland 2001; Hamilton 2005).

The UN Convention on Biological Diversity (1992) defines biological diversity as *"variability among living organisms from all sources [...], including diversity within species, between species and of ecosystems".*

This definition includes already two divergent approaches that emerged in the second half of the twentieth century, the community ecology and the ecosystem ecology (Loreau 2010). Community ecology focuses on species diversity and the forces that regulate diverse communities. It combines genetic diversity, the sum of genetic information of plants, animals and microorganisms (Barthlott *et al.* 1996; Dodson *et al.* 1998; Gaston & Spicer 1998), and organismal diversity (Mönkkönen 1994; Dodson *et al.* 1998; Gaston & Spicer 1998) that incorporates also processes maintaining the various aspects of variation in nature.

Whereas ecosystem ecology focuses on the overall functioning of ecosystems, including energy fluxes and nutrient cycles (Loreau 2010) and to the broad variety of habitats, biotic communities, and ecological processes within ecosystems. Therefore biodiversity is an "umbrella concept" (McNeely *et al.* 1990) which encompasses all five living kingdoms (Dodson *et al.* 1998).

The importance of biodiversity from a human point of view lies in its direct and indirect contributions towards human well-being of *ecosystem services* (Srivastava 2002). These services, subdivided in four categories, provide "supporting services" (e.g., nutrient cycling), "provisioning services" (e.g., food, water, energy), "regulating services" (e.g., carbon sequestration, decomposition), and "cultural services" (e.g., recreational areas) (UNEP 2005b; for a thorough review see Cardinale *et al.* 2012). McNeely *et al.* (1990) categorize them in an economic way as "consumptive use value" (e.g., firewood and fodder), "productive use value" (commercially harvested goods, e.g., timber and fish) and "non-consumptive use value" (indirect ecosystem functions, e.g., watershed protection and photosynthesis). Evidence suggests that species extinction has a negative effect on these biodiversity values (Ghilarov 2000).

1.2.2 Distribution of biodiversity

Biodiversity is distributed heterogeneously across the Earth (Gaston 2000). In general, global biodiversity shows a latitudinal and an altitudinal diversity gradient with decreasing species from the equator towards the poles (e.g., von Humboldt 1807; Darwin 1859; Wallace 1878; Fischer 1960; McIntosh 1985; Stevens 1989; Rosenzweig 1995; Gaston 1996b, 2007; Brown & Lomolino 1998; Willig 2001; Whittaker *et al.* 2001; Hillebrand 2004; Lomolino *et al.* 2010). Biodiversity is generally high in hot and humid places (Storch *et al.* 2007). This has been documented for morphologically different taxonomic groups like microorganisms, trees, insects and primates (Stevens 1989). Even if these findings were published already more than a century ago, the causes of this gradient have not been clearly justified until now (Shmida & Wilson 1985; Rohde 1992; Chown & Gaston 2000; Mittelbach *et al.* 2007). It seems that it does not count for all taxa (e.g., grasses, Whittaker *et al.* 2001) and the underlying control of this trend is still "unexplained" (Taylor & Gaines 1999).

Numerous hypotheses have been advanced to account for the observed gradient of species richness from the equator to the poles but none provides a complete picture (Field *et al.* 2009). For example Willig *et al.* (2003) list over 30 hypotheses that try to explain the latitudinal gradients of biodiversity. The big variety of analyses of the latitudinal gradient show different foci and extends (Willig 2001) which makes them difficult to compare. Especially on global scale it is difficult to gain representative data to analyze (Austin 1999). Schemske (2002) sees latitudinal gradients of diversity as ultimately dependent on the historical, geographic, biotic, abiotic, and stochastic forces and therefore biodiversity is connected to their ecosystems.

A first map of global diversity was published by Malyshev in 1975. In 1996, Barthlott *et al.* published a more precise one on basis of more than 1400 floras and floristic studies and which was modified in 2005 (Barthlott *et al.* 2005) (Figure 1-1). Further maps have been published by Kreft & Jetz (2007).

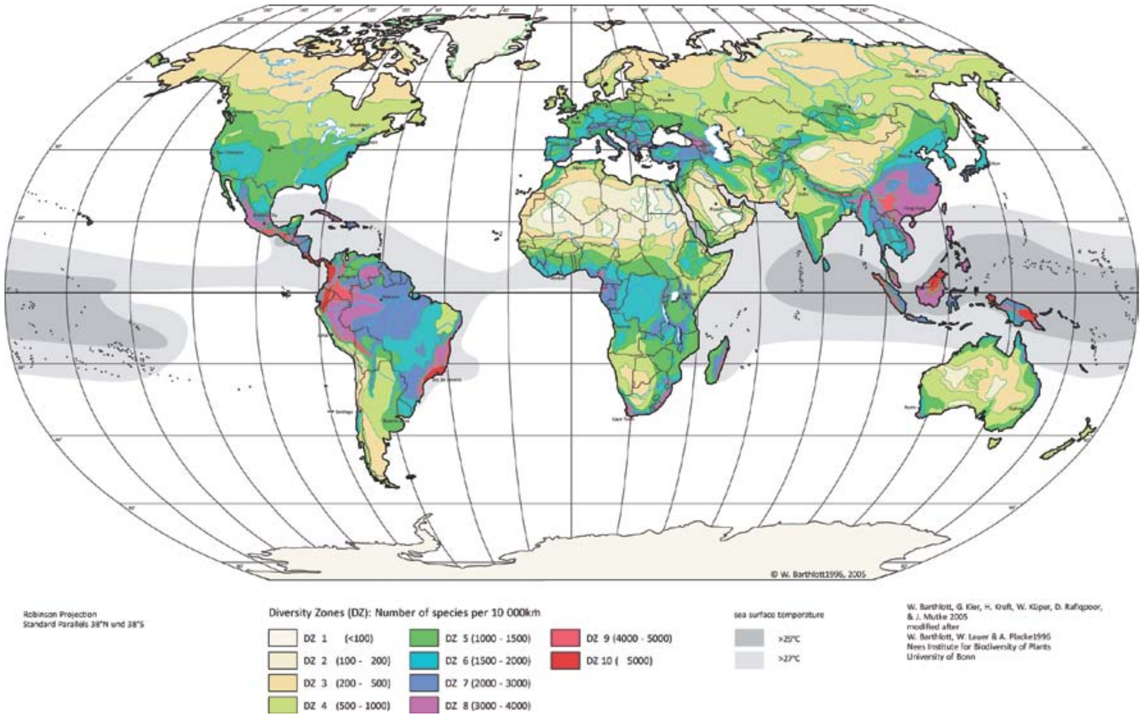


Figure 1-1: Map of global biodiversity. Colors indicate numbers of vascular plants. Source: Barthlott *et al.* 2005.

Gaston (2000) determines four areas of enquiry in broad-scale spatial variation in biodiversity: latitudinal gradients in species richness, species–energy relationships, relationships between local and regional richness, and taxonomic covariance in species richness. Moreno-Rueda & Pizarro (2007) see three primary reasons for species richness, the heterogeneity of the environment, the climate, and human influence. Heterogeneity creates niches that influence species distributions (Brown 1995; Pulliam 2000; Wiens & Donoghue 2004) and the quantity of ecological niches within an area supports the coexistence of species. The climate is in fact part of the "water-energy-hypothesis" and was originally linked to the latitudinal gradient (O'Brien 1993, 2006; Francis & Currie 2003; Hawkins *et al.* 2003; Hillebrand 2004) but also proven for the elevation gradient (e.g., Marini *et al.* 2008). According to this hypothesis, species richness is controlled by climatic factors like the temperature or water- and humidity-related variables in the tropics (Hawkins *et al.* 2003; Currie *et al.* 2004; Field *et al.* 2005). Primary production is directly linked to temperature and precipitation (Waide *et al.* 1999; Chown *et al.* 2003) and plant species richness shows peaks under heat in cold areas but a higher variance in warm areas (Francis & Currie 2003; Li *et al.* 2013). Outside the warm and humid part of the world and towards the poles also frost and drought may play an important role (Currie *et al.* 2004; Wiens & Donoghue 2004).

Field *et al.* (2009) conducted a meta-analysis in grouping the available hypotheses into six:

1) Climate/productivity: such as precipitation, evapotranspiration, temperature (e.g., Currie 1991; Hansen & Urban 1992; Whittaker 1999; Gaston 2000; Kleidon & Mooney 2000; Francis & Currie 2003; Venevsky & Veneskaia 2003; Gillman *et al.* 2013)

2) Environmental heterogeneity: such as number of habitats, topographic relief, abiotic disturbance (e.g., Shmida & Wilson 1985; Ricklefs 1987; Fédoroff *et al.* 2005; Tews *et al.* 2004; Waldhardt *et al.* 2004).
3) Edaphics/nutrients: such as soil structure, substrate or water quality, pH (e.g., Marini *et al.* 2007; Cousins 2009; Matthews *et al.* 2009)
4) Area: such as plot size, habitat size, island or geographic region (e.g., Rosenzweig 1995; Heegaard *et al.* 2013)
5) Biotic interactions: direct or indirect effect of species, such as competition and shading (e.g., Kreft & Jetz 2007)
6) Dispersal/history: such as patch connectivity for dispersal possibility, but also geological and climatic history, such as tectonic, long-term climatic stability (e.g., Ricklefs 1987; Dynesius & Jansson 2000; Webb *et al.* 2002; Jetz *et al.* 2004; Qian & Ricklefs 2004; Wiens & Donoghue 2004).

1.2.3 Scale of biodiversity

Spatial and temporal scales play an important role in the geographic variation and therefore for species richness (Sousa 1984b; Francis & Currie 2003). Wiens complains in 1989 that scientists neglect the differences of scales in their research (Wiens 1989), and even in 2001 Whittaker *et al.* see that a "general weakness in the ecological literature is the failure to distinguish factors relevant to particular scales of analysis" (Whittaker *et al.* 2001, p. 454). A decade later, countless scientific studies address and design their research on the appropriate scale, but e.g., for plants, the overall importance of the landscape context is still somewhat unclear (Öster *et al.* 2007). Many studies show no or weak effects of the landscape contexts (Eriksson *et al.* 1995; Honnay *et al.* 1999; Söderström *et al.* 2001; Dupré & Ehrlén 2002; Dauber *et al.* 2003; Weibull & Östman 2003). Hewitt *et al.* (2010) state that patterns that are apparent at one scale can collapse to noise when viewed from other scales.

Several studies prove the positive influence of productivity, or available energy, on species richness on larger scales (e.g., Harrison *et al.* 2006; Field *et al.* 2009; Šímová *et al.* 2013). Also climatic variables increased their effect with increasing spatial extend (Siefert *et al.* 2012). According to Austin (1999) and Kreft & Jetz (2007), the spatial heterogeneity has a stronger influence on plant species richness than the area effect on regional scale. Depending on their heterogeneity, larger areas contain more individuals, more habitats, and more biomes than smaller areas (Rosenzweig 1995; Crawley & Harral 2001). Several small spread habitat patches usually contain more plant species than a few large habitat patches, as indicator for a different availability of resources and therefore a support for the establishment of plant species (Margules *et al.* 1994; Honnay *et al.* 1999). On the other side, larger areas promote dispersal because they provide larger populations and therefore more dispersers, and moreover make bigger targets for new species (Cornell & Lawton 1992; Skelsey *et al.* 2013).

Sankaran & McNaughton (1999) found evidence that at larger ecological scales rather extrinsic determinants of biodiversity (e.g., disturbance regimes and site history) may be the primary determinants for community stability. Rosenzweig (1995) furthermore included the time frame in his research and saw a determination of species richness by rates of speciation and extinction at the largest spatial scales and over the longest time scales.

At local scale (some square meters to some hectares), Qian & Ricklefs (2004) found proof for constraining environmental factors which replace the influence of regional processes (Grime 1973; Huston 1979; Tilman 1982; Grace 1999). Edaphic factors increase their influence on plant community composition with decreasing spatial grain (Siefert *et al.* 2012). Also biotic interactions determine species distribution on small scales (Bisigato *et al.* 2009; Wiens 2011; Le Roux *et al.* 2013) by "birth, death, and dispersal rates of individuals interacting with populations of competitors, mutualists, and natural enemies" (Pacala 1997).

But also the heterogeneity plays an important role at small scales with differences in resource availability (light, nutrients) or punctual disturbances (grazing, nutrient input), to name only a few (Quilchano *et al.* 2008). Still some authors (e.g., Ricklefs 1987; Caley & Schluter 1997; Bisigato *et al.* 2009) see a connection between the scales. They see a strong influence of the regional diversity on local diversity.

The Swiss "Biodiversity Monitoring" program (Weber *et al.* 2004) for example accounts for the scale problem with the implementation of three different spatial scales, following the recommendations of Whittaker *et al.* (2001). In ecology these three components of species diversity are recognized as (1) local species richness or within-habitat diversity (alpha diversity), (2) regional species richness (gamma diversity) and (3) spatial turnover or differentiation diversity (beta diversity) (Whittaker 1960, 1972; Cody 1975; Pimm & Gittleman 1992; Whittaker *et al.* 2001; Tuomisto 2010a).

1.3 NATURAL PROCESSES THAT INFLUENCE ECOSYSTEMS

Natural processes lead to a landscape with heterogeneous structure (Andrén 1994). There are two interacting classes of processes, continuous and discrete (Hobbs *et al.* 2006). Continuous processes for example include birth, death and migration of species and competition between them, accumulation of biomass, and succession. Discrete processes are disturbances like fire (Wright 1974; White 1979; Pickett & Thompson 1978; Baker 1995; Buhk *et al.* 2007a), windstorms (Connell 1978; Foster 1980) and floods (Biggs 1995). They often influence the continuous processes (Jentsch 2001) and affect community structures and dynamics (Sousa 1984a; Pickett

1998; Reynolds *et al.* 1993; Turner *et al.* 1998; Borics *et al.* 2013). They also influence competition (White & Jentsch 2001) and landscape functions, like energy partitioning and hydrologic flows (Ryszkowski 1992), and temporarily decrease the buffering capacity of ecosystems to natural environmental fluctuations (Odion & Sarr 2007).

The most cited definition for disturbance says, a disturbance is "an event in time that disrupts the ecosystem, community or population structure and changes the resources, substrate availability or physical environment" (White & Pickett 1985). Another definition says that a disturbance is "an event which alters the niche opportunities available to the species in a system" (Shea & Chesson 2002; Shea *et al.* 2004). Disturbances vary in frequency and intensity and can be small scaled with little impact or even force an ecological reset of a landscape (Wright 1974; Horn 1976). This reset is often called "novel" (Chapin & Starfield 1997; Hobbs *et al.* 2009) or "emerging" (Milton 2003) ecosystem, and in this context mostly related to climate change or invasive species.

However, disturbance is indispensable to the survival of many species (Walker *et al.* 1999; Jentsch 2007) and has an important influence on ecosystem processes like primary and secondary production (Sousa 1984a). There are important effects of disturbances to plant communities: the effect of extinction for some plant individuals on one side, but also the chance to establish new communities as a positive factor (Denslow 1980; Pickett & White 1985; Rosenzweig 1995). At a certain intensity, disturbances prevent a competitive exclusion and thus a coexistence of several species (Grime 1973; Petraitis *et al.* 1989; Hughes *et al.* 2007). According to Roberts & Gilliam (1995), these effects are a key factor to maintain biological diversity. A correlation between natural disturbances and species richness has been proved by several scientists (e.g., Grubb 1977; Connell 1978; Grime 1979; Huston 1979; Pickett 1980).

1.4 ANTHROPOGENIC INFLUENCE

Called the single greatest threat to biological diversity, land transformation and establishing monocultures have resulted in loss and fragmentation of habitats in many different ecosystem types (Vitousek *et al.* 1997) and are considered to be some of the main drivers behind species loss, regionally and globally (Tilman 1994; Wiens 1995; Wiens 1995; Lindborg & Eriksson 2004a; UN 2008; Schindler *et al.* 2008). Fragmentation often facilitates additional negative consequences to species and ecosystems beyond the simple loss of habitat, in concert with other processes, like the increasing isolation and reduction of patch size (Andrén 1994).

The Human Footprint Analysis (http://sedac.ciesin.columbia.edu/data/collection/wildareas-v2) estimated more than 80% of the land surface being either directly or indirectly affected by human influences and natural disturbances have been replaced by human impacts in many places (Baker 1995; Ernoult *et al.* 2003) and patterns of once pristine nature are now overlaid by human-dominated landscapes (Tscharntke *et al.* 2012). Land use change involves two main impacts on the biosphere: conversion (i.e. natural habitats altered for human use) and intensification (e.g., greater intensity and/or frequency of disturbance, increased use of external inputs - Foley 2005). The structure of a landscape is changed by (1) the fragmentation or even destruction of habitats, (2) the change of availability or quality of dispersal possibilities, and (3) a reorganization of patches (Fahrig & Merriam 1994, 2003).

Transition from wild lands to agricultural use over the past several hundred years has reduced previously forested lands by 20 to 50% (Matthews *et al.* 2000). Especially during the Bronze Age, large areas of open grassland systems were established, e.g., in the southern part of Germany (Poschlod & Baumann 2010; Eriksson 2012). According to White *et al.* (2000), 25% of grasslands have been converted to cropland. Analyses show that biodiversity has continued to decline over the past four decades, with most state indicators (e.g., species' population trends, condition) showing negative trends (Butchart *et al.* 2010). In the style of geologic ages the current era is therefore called the "Anthropocene" (Crutzen 2002; Zalasiewicz *et al.* 2011).

Ecosystems are complex, dynamic systems with interactions between nutrients, plants, animals, soils, climate, and many other components (Blois *et al.* 2002; DeFries *et al.* 2004). Land-use change may lead to a reduction in biodiversity, soil and water pollution through the use of fertilizers and pesticides, soil sealing and compaction, and altered hydrological, nutrient and atmospheric cycles (e.g., Pimm & Raven 2000; Foley 2005; van Asselen & Verburg 2013). Conversion of land alters a range of other ecosystem functions, such as the provisioning of freshwater (e.g., Palmer *et al.* 2002), regulation of climate (e.g., Dale 1997; Díaz *et al.* 2005), biogeochemical cycles (e.g., Huth *et al.* 2012), mass and energy fluxes (e.g., Dale 1997), maintenance of soil fertility (e.g., Hartemink 2010), and habitat for biological diversity (DeFries *et al.* 2004). Land-cover changes also affect regional climates through changes in surface energy and water balance (Pielke *et al.* 2002; Kalnay & Cai 2003).

As direct small scaled and local effect, these disturbances influence competition, substrate and resource availability (Jentsch 2001) and therefore have a strong effect on plant species, which might be reduced or some species even disappear locally (Bagaria *et al.* 2012). Changes occur in abundance, community structures and composition, especially in small, fragile, or already stressed populations and on small scaled patch-levels (Huston 1979; Rykiel 1985; Mazerolle & Villard 1999; Jentsch 2001; Lindborg *et al.* 2005; Watling & Donnelly 2006).

Forman (1995a, in August *et al.* 2002) analyzed the speed of impact of selected disturbances/land transformations on different scales. Direct, fast effects are found e.g. after forest cutting, wetland drainage, and application of herbicides. Slower and mostly direct impact show e.g. reforestation, burning, and flooding. Release of non-native species may have direct or indirect effects.

Changes in species diversity and composition after habitat disturbance are dependent on spatial scale (Jentsch 2001; Dumbrell *et al.* 2008) and patch dynamics (Loucks 1970). Depending on the kind and extend of disturbance the result can be very different. A small scaled disturbance generates gaps within the “preexisting background assemblage of organisms” (Sousa 1984a). These spots of damaged or removed vegetation layer create space for succession and new species and lead to a heterogeneous landscape (Loucks 1970). Therefore, disturbances play a key role in shaping a landscape since they modify resource availability and influence competition (Blois *et al.* 2002). According to Whittaker (1953), one characteristic of a natural landscape is the mosaic of successional patches of various sizes. Succession and recolonization begins within short time after the disturbance (Sousa 1984a), even after large scale, or “catastrophic disturbances without survivors” (Platt & Connell 2003). The removal of dominant species may lead to an increase of other species, even if they would occupy the same ecological niche similar to the previously dominant species (White & Jentsch 2001). On global scale, Sax (2003) sees a decline of species diversity with habitat destruction and the introduction and dispersion of exotic or invasive species since they suppress or even replace native species (Diamond *et al.* 1989). This also happens on local scale, but biological and physical interactions play a more important role and therefore show a mixed effect on diversity. To examine landscape patterns thus helps to understand biodiversity (Ernoult *et al.* 2003).

Important for local plant diversity are the permeability of the landscape (Honnay *et al.* 2002), the ability for dispersal (Hester *et al.* 1991) and the physical environment (nutrients, soil moisture, substrate) (Pollock *et al.* 1998).

1.4.1 Cultural landscape

In a human dominated landscape, the question arises if these hypotheses and theories withstand. The long history of agriculture and the transformation of dense forests into a heterogeneous and mosaic landscape enhanced biodiversity in Central Europe (Waldhardt *et al.* 2003). This is particularly true for vascular plants (Sukopp 1977 in Waldhardt *et al.* 2003).

Still, even the ‘traditional landscape’ has been shaped by humans for thousands of years and should therefore not be romanticized (Widgren 2012) because it has always been part of the cultural landscape (Eriksson 2012) and is not per se a synonym for ‘low-intensive land use’ (Bignal & McCracken 1996). Consequently, Sprugel (1991) asks, where one should place a ‘benchmark’ when a landscape was in natural state? However, the metamorphosis from a natural to an industrial landscape with large areas dominated by agribusiness and forestry in monocultures, which started in the middle of the 20th century (Waldhardt *et al.* 2003; Hopkins 2009), has led to a change of vegetation: the promotion of few high-yielding plant species on fields and in forests for commercial purposes (Matson *et al.* 1997; Boatman 2005). This preference of few plants correlates with the intentional exclusion of unwanted species and leads to a "planned diversity" (Matson *et al.* 1997).

Several important factors influence species richness in forests and on arable fields that goes far beyond monocultures. There are the usage of agrochemicals that directly affect structure and diversity of vegetation (Andreasen *et al.* 1996), but also of invertebrates (e.g., Haughton *et al.* 1999) and birds (e.g., Donald *et al.* 2001). Numbers of European farmland birds have been reduced by 30% due to the land-use change into cereal fields (Donald *et al.* 2001). In agricultural landscapes the specialization of farms and the join of former small farms to economies of scale lead to a large-scale and very efficient management (Meeus 1993; Stoate *et al.* 2001; Robinson & Sutherland 2002). The establishment of cropped areas removes small habitat structures, like ponds, hedgerows, and scrubs (Robinson & Sutherland 2002; Benton *et al.* 2003; Hopkins 2009; Hartel *et al.* 2013). These structures have the function of species pools, corridors, shelters, nest sites (Benton *et al.* 2003; Smart *et al.* 2006), but also have importance for ecosystem services, like pollination or slope stability (García-Feced *et al.* 2014) and therefore can compensate some negative influence of land use practices (Liira *et al.* 2008; Fahrig 2003). But the uniformity is not only based on spatial but also on temporal extend. The season of productivity has been prolonged and "threshold dates" (Benton *et al.* 2003, 185) are set for fertilizing and harvesting (Bignal *et al.* 2001). In addition, moment and quantity of mowing influence plant species community (Kramberger & Kaligaric 2008).

Though, also grasslands undergo a commercial improvement. In killing weeds, applying higher-yielding seed and increasing silage production with fertilizer input a majority of plant species cannot establish (Vickery *et al.* 2001). Harvesting influences the natural seasonal rhythm of plant species, especially in case of multiple mowing per year (Ignatavičius *et al.* 2013). The area of agricultural unimproved grassland, i.e. grassland that has never been subject to fertilization and intensive haymaking and grazing (Stoate *et al.* 2001; Vickery *et al.* 2001), shows a more than 90% decline between 1930s and 1980s in the UK (Fuller 1987). One context could be the production rate of less than 50% on semi-natural grasslands (Hopkins 2009).

1.4.2 Semi-natural / natural areas

Human influence on nature has been lasting for thousands of years. Grazing of domesticated herbivores, mowing for hay, logging for constructions and firewood and farming has shaped the landscape but also the assemblage of organisms (Motzkin *et al.* 2002; Pärtel *et al.* 2005). Van Dijk (1991) invented the term "semi-natural grassland". This term incorporates a human meliorated landscape but also a landscape that in somehow retains the predominance of native species (Hopkins 2009). These semi-natural landscapes are leftovers of historical rural landscapes (Eriksson *et al.* 1995; Bullock 2011; Johansson *et al.* 2011) and thus species and communities are dependent on disturbances (Foster 2002; Bullock 2011), like the traditional extensive grazing (Luoto *et al.* 2003). Studies have been conducted in several countries all over Europe (e.g., The Netherlands: Snoo *et al.* 2012; Sweden: Cousins *et al.* 2007; Finland: Arponen *et al.* 2013; Norway: Auestad *et al.* 2008; Italy: Burrascano *et al.* 2013; Poland: Kramberger & Kaligaric 2008; Austria: Pötsch & Krautzer 2009) and cross-national (e.g., Plieninger *et al.* 2006; Billeter *et al.* 2008; Emanuelsson 2009a; Beaufoy *et al.* 2011). They all conclude that changing land-use practices have diminished the area covered by semi-natural landscapes and therefore undergo a decrease in species richness. Snoo *et al.* (2012) compared agricultural grasslands and nature reserves and found 87% more species in the natural landscape. Besides the landscape diversity, the openness of a landscape positively supports species diversity (Meltsov *et al.* 2011). Especially the higher structured semi-open areas show a greater diversity than pure open landscapes or forests (Emanuelsson 2009a; Billeter *et al.* 2008; Eriksson 2012). Liira *et al.* (2008) find evidence for highest correlation between the composition of plant functional groups and the availability of semi-natural and natural habitats.

Silviculture has become more intensive due to high technology harvesting machinery. Monocultures often consist of not adapted, or exotic and fast growing species (Young *et al.* 2005), covering large scales of the landscape in even-aged stands (Gamborg & Larsen 2003). However, scientific findings drift apart about their ecological status (Brockerhoff *et al.* 2008). Contrary to the general perception, numerous studies in monocultures show habitat for numerous species (plants, animals, and fungi, also endangered species) (e.g., Carnus *et al.* 2006). Even diseases (Chou 1981) and insect outbreaks (Bain 1981) are not necessarily more frequent in plantations. Albrecht *et al.* (2012) analyzed the correlation between forestry and storm damage in Germany. They found out that tree species (high risk: spruce, Douglas-fir; low risk: beech, oak) and stand height have a major influence on the risk of storm damage.

One important factor is the time since planting. Typical species assemblages will develop rather in older and more heterogeneous stands than in young plantations and deadwood gives habitat for insects and fungi (Brockerhoff *et al.* 2008). Even the theory that fragmentation of a forest that isolates patches, will lead to a risk of extinction of species, is increasingly diluted (Fischer & Lindenmayer 2006).

1.5 MOST RELEVANT HYPOTHESES IN DISTURBANCE ECOLOGY

The question arises, if large, infrequent disturbances show different effects than small, frequent disturbances (Romme *et al.* 1998). Turner *et al.* (1998) see the frequency and magnitude of a disturbance as inversely related; events with small magnitude occur frequently, events with a large magnitude occur seldom (Figure 1-2). However, there must be a minimum of impact to be considered as disturbance.

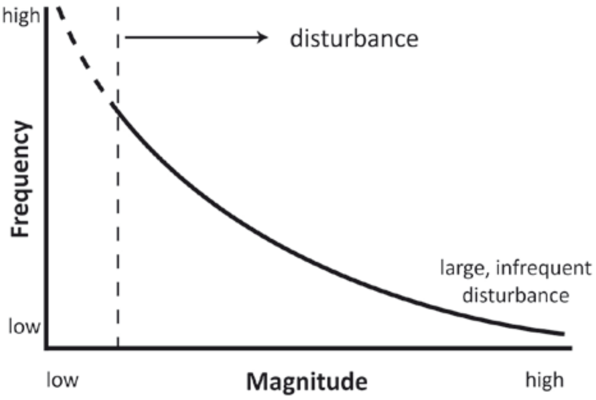


Figure 1-2: Magnitude and frequency of disturbances are mostly reciprocally proportional related. Event with large magnitude are seldom, the ones with low magnitude are frequent. A minimum of magnitude is required to be considered as disturbance. Modified from White & Jentsch 2001.

But not only the magnitude but also duration and abruptness play an important role in disturbances (Figure 1-3). The interaction of the abruptness and magnitude reduces the biomass (or other physical variables). Depending on the body mass and life span of the organisms the disturbance can be critical or moderate. After the disturbance the variable returns to the similar dynamics before the disturbance (Borics *et al.* 2013).

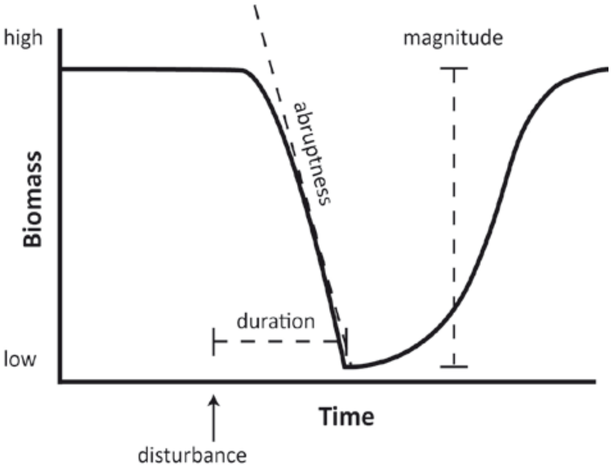


Figure 1-3: Abruptness, duration and magnitude: Three factors that define disturbances. Modified from White & Jentsch 2001.

Collins *et al.* (1995) give an example of fire as disturbance in grasslands. They see a greater impact of the frequency than the intensity of a fire. Recurring disturbances interact with the different stages of succession. The frequency determines if a disturbed area is and stays occupied by early successional species or will be dominated by slower but competitively dominant species (Petraitis *et al.* 1989; Collins *et al.* 2001). According to Huston (1979), disturbances that recur more often than the time needed for competitive exclusion in succession maintain the species richness of an area.

The following graph shows the connection between the intensity and frequency of disturbances and the successional response (Figure 1-4). Using the example of biomass removal at low frequency and intensity, there is just little vegetation damage and therefore only little succession possible. At high frequency but low intensity of disturbances, patches might be created that can be occupied by the same or different species but with little successional change (Cain *et al.* 2008). The other end of the spectrum shows a massive disturbance but the low frequency indicates a rare event, like the eruption of a volcano. This "catastrophic disturbance without survivors" (Platt & Connell 2003) affects the entire community and primary succession of the whole area will reassemble the community.

However, an intermediate intensity and frequency will cause some damage with some, but not all individuals being destroyed. This leads to a reestablishment of the community by secondary succession.

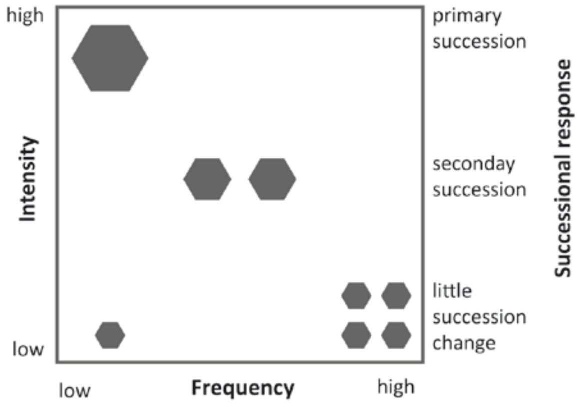


Figure 1-4: The spectrum of disturbance from low to high intensity and low to high frequency, and the successional response (modified from Cain *et al.* 2008). At high intensity and high frequency (plant) communities cannot establish.

These findings are expressed in different hypotheses. One of or even the most recognized hypothesis is the **Intermediate Disturbance Hypothesis (IDH)**, which is assigned to Grime (1973) and Connell (1978), but can be traced back to Eggeling (1947) and Hutchinson (1953) (origin discussed in Svensson *et al.* 2012). The hypothesis states that the relationship between biodiversity and disturbance depends on the intensity of disturbance (i.e. frequency, duration, size) and time lag since disturbance happened.

Short after high disturbance pioneer species dominate. Diversity is low because of the short time for colonization. On the other side, at low impact or long time after a disturbance competitively dominant species replace r-strategists. However, at moderate level these dominant species are suppressed, which facilitates also the colonization of less-competitive species. Species diversity is maximized because of the coexistence and shows a unimodal relationship (Figure 1-5).

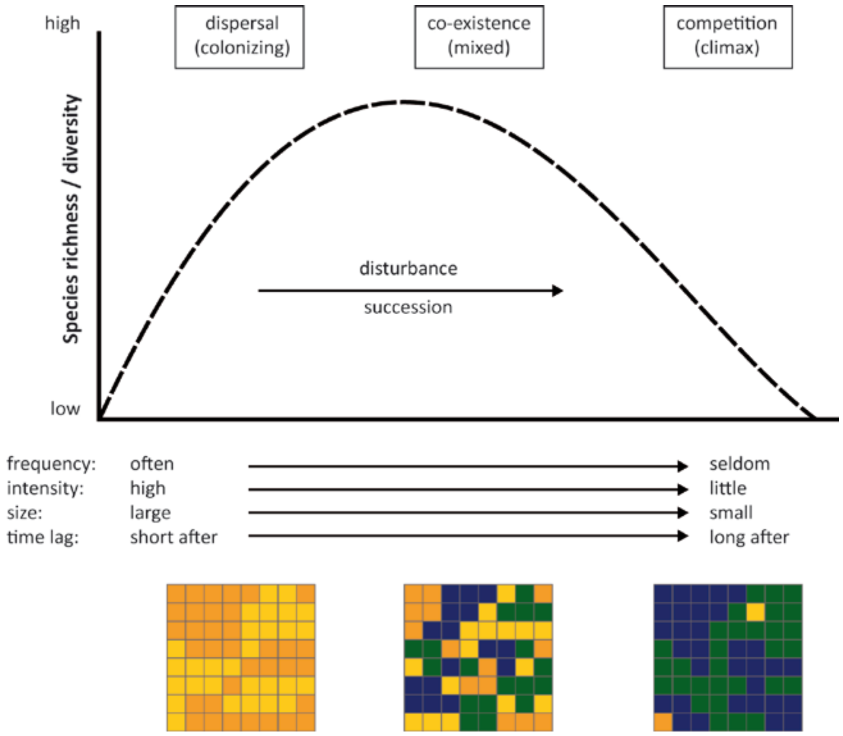


Figure 1-5: Intermediate Disturbance Hypothesis according to Grime (1973) and Connell (1978). Left: High frequency, high intensity or large extent of a disturbance, or short after disturbance event: Species diversity is low because only good colonizers or highly tolerant species can persist. Right: Low frequency, low intensity, or small sized impact of disturbance, or long time after disturbance event: Species diversity is low at low disturbance frequency because of competitive exclusion. Center: Species diversity is higher at intermediate disturbance frequency, since colonizers and competitors mix.

This theory is controversially discussed. Numerous studies were conducted but show results that either support (e.g., Mackey & Currie 2001; Martín-Queller *et al.* 2011) or refute (e.g., Svensson *et al.* 2012; Fox 2013b) the IDH.

In looking at the hypothesis the question arises, if an ecosystem can actually be in equilibrium state. According to Wiens (1989), it depends on the scale of observation and "may show characteristics that correspond to a relatively stable, equilibrium state". Reynolds (1993) and Hughes *et al.* (2007) state that disturbances prevent the internally-driven progress towards an ecological equilibrium.

Huston (1979) extended the IDH with the assumption that species diversity depends on productivity to the **Dynamic-Equilibrium Model (DEM)**. Succession after disturbances needs to have a certain growth rate. At lower productivity rate, a weak disturbance is sufficient to reset the process again. At high growth rates and low disturbance, dominant species outcompete less dominant species, whereas in turn at high disturbance, dominant species are reduced (Ödman *et al.* 2012). Hence, at intermediate productivity rate, species diversity in maximized. Many ecologists (e.g., Connell 1978; Petraitis *et al.* 1989; White & Jentsch 2001; Sarr *et al.* 2005a, 2005b; Odion & Sarr 2007) see the non-equilibrium caused by disturbances as very vital for species diversity because of the competition process on different scales.

Numerous studies see a positive relation between environmental heterogeneity / landscape diversity and plant species richness in forests (e.g., Decocq *et al.* 2004; Sarr & Hibbs 2007), grassland (e.g., Økland *et al.* 2006; Öster *et al.* 2007), riparian wetlands (e.g., Pollock *et al.* 1998), and farmlands (e.g., Duelli 1997; Benton *et al.* 2003; Weibull & Östman 2003).

Several hypotheses have been advanced to explain the correlation between a heterogeneous landscape and species richness. **Habitat Heterogeneity Hypothesis** (MacArthur & MacArthur 1961; MacArthur & Wilson 1967, for review see Tews *et al.* 2004) and **Habitat Diversity Hypothesis** (sensu Shmida & Wilson 1985) see enhanced species richness in more diverse landscapes because of the availability of more niches and habitats, which was supported by Atkinson & Shorrocks (1981). Additionally, a highly diverse landscape increases the pool of species (Pärtel *et al.* 1996; Dupré *et al.* 2002). Also the **Mosaic Concept** (Duelli 1997), which was applied in agricultural landscapes relates floristic richness to the number of habitat patches in mosaic landscapes.

Based on the intermediate disturbance hypothesis and a literature review of Mackey & Currie (2001) that states, that only 19% of the studies show a peak of species diversity at intermediate disturbance, Warren *et al.* (2007) noticed that the diversity or heterogeneity of disturbances need to be included and framed the **Heterogeneous Disturbance Hypothesis (HDH)**. The HDH suggests, that "biodiversity is maximized where multiple kinds, frequencies, severities, periodicities, sizes, shapes, and/or durations of disturbance occur concomitantly in a spatially and temporally distributed fashion" (Warren *et al.* 2007, 610). Therefore heterogeneity of disturbances manifolds conditions for coexistence of species.

However, anthropogenic disturbances can also have a very different effect within a region, the **biotic homogenization** of species (McKinney & Lockwood 1999). This means that formerly distinct species communities become increasingly similar in composition (UNEP 2005a; Olden & Rooney 2006). Three forms of homogenization have been identified: i) functional homogenization, ii) taxonomic homogenization, and iii) genetic homogenization (Olden *et al.* 2004). Clavel *et al.* (2011) in particular see functional homogenization as important indicator for changes in biodiversity and an important factor for ecosystem services.

Homogenization is not a surprising and new phenomenon but has been accelerated by human activities (Elton 1958). Transport of goods and people around the globe and the introduction of alien species into regions where they are not native on one side, and the local extinction of native species through land-use change and habitat loss on the other side are the major drivers (UNEP 2005a; Lambdon *et al.* 2008). The consequences depend on the potential of threatening the native species.

Olden & Poff (2003) see this homogenization effect associated in disturbed environments with changes in the natural colonization and extinction rates. Furthermore it seems to be enhanced especially by the large geographic range of invasive non-native species (Fleishman *et al.* 2005; McKinney & La Sorte 2007). Cosmopolitans expand their range ("winners"), and native and endemic species reduce theirs ("losers") (Baskin 1998; Olden *et al.* 2004).

But even in unfragmented landscapes, homogenization takes place and it has not been proved yet, that fragmentation of habitats leads to homogenization (Dormann *et al.* 2007a). Rooney *et al.* (2004) found evidence for a decline of 18.5 % of native plant species in forest understory communities in 62 forest stands (20 m² scale) within 50 years. In the same time, 80% of all plots showed an increase of the ratio of alien plant species. Specialized and rare species, which have a high contribution to species diversity of a landscape, become substituted by generalists (Wagner & Edwards 2001).

Clavel *et al.* (2011) saw evidence for this vulnerability of specialists in the concept of ecological niche (Hutchinson 1957). The **niche theory** tries to explain the coexistence of species. It says that two species cannot occupy an identical ecological niche in a stable equilibrium at once. A competition between these two species for the same resources would either lead to a local extinction of the less dominate one or a shift to a different ecological niche (competitive exclusion principle; Grinnell 1904; Gause 1932; for more information see Chase & Leibold 2003).

Whereas a different theory, the **neutral theory** (Hubbell 2001; Rosindell *et al.* 2011) states, that this competitive exclusion mostly takes too long and therefore other processes must happen or even dominate. These can be speciation or dispersal abilities of species. Whittaker (1965) sees the "evolution of both niche and habitat differentiation" (Whittaker 1965, 259) as reason for a coexistence. Furthermore Hubbell invokes "chance" as explanation. Hence, two or more species can potentially coexist within the same trophic category ('guild'; Mikkelson 2005).

Both theories provide complementary strengths and weaknesses (Chave 2004; Mikkelson 2005) and it is suggested either to reduce the theories to the processes that are being explained best, or, preferably combining them (Mikkelson 2005; Leibold & McPeek 2006). Haegeman & Loreau (2011) conducted a mathematical synthesis in combining the niche theory in using the Lotka-Volterra competition equations and Hubbell's neutral theory but admit the restriction to a single local community.

Fact is that we cannot focus on one single landscape structure or land use type but have to see the whole assembly of land uses in one picture. Species composition and communities are influenced by the surrounding landscape (Weibull & Östman 2003) and will differ substantially between intensively managed agricultural landscapes and semi-natural areas. Cousins & Aggemyr (2008) found that a field encircled by a commercially managed forest exhibited 35% more plant species than these fields that were encircled by farmed landscapes. Intensively used landscapes, like these of Central Europe, already show changes in land uses and land-use intensities on local to regional scales. Numerous studies have been conducted concerning land-use change, the influence of land use and single disturbances on species diversity (e.g., fire, agriculture, pesticides, wind throw, etc.) and differences between anthropogenic marked landscapes and natural or semi-natural habitats.

1.6 THESIS OUTLINE

The general aims of my thesis are the recognition and the appointment of processes and patterns in a multiple disturbed cultural landscape. While most scientific studies neglect the complexity of a disturbance regime and focus on only one or few parameters, this study goes far more into detail in deliberately including all detected land-use and disturbance types. Additionally to these different types, each single parameter was further explained by temporal (frequency, duration and season) and spatial (size, form and distribution) characteristics of their occurrence and a selection criterion for tree removal (species, age and location) according to Buhk *et al.* (2007b).

With my extensive data I expect to find an explanation for the influence of land-use and disturbance-intensity gradients on plant species richness that characterize the three study sites, stressing that despite their different types of landscape and land-use intensities, they are located nearby. Therefore they represent a cross selection of land-use intensities in a cultural landscape under the same climatic circumstances.

The three study sites show a variation of nearly none to very high anthropogenic impact and differ in their history. Since species richness is correlated with anthropogenic impacts, changing circumstances reduce species richness and increase the number of threatened and endangered species. Furthermore, non-native species gain importance, especially in a globalized and disturbed world. With my data analyses I furthermore expect to find answers, where and why these species appear and where a homogenization of the flora by widespread species occurs.

This should lead to the identification of valuable and worth to be protected areas and their specific land use and disturbance regime. These results may be used as additional component for conservation issues in cultural landscapes. On basis of these data, I furthermore test several ecological hypotheses.

Use of terms

Landscape: The study site of 'Grafenwöhr Military Training Area' mainly belongs to the natural region of Upper Palatine Hills (Oberpfälzisch-Obermainisches Hügelland, D62) but intersects with the nature region of the second study site, 'Frankenalb', in the Franconian Jurassic (Fränkische Alb, D61). The study site of 'Fichtelgebirge' is situated in the Thuringian-Franconian low mountain range (Thüringisch-Fränkisches Mittelgebirge, D48) (Ssymank 1994). On larger scale, they all belong to the ecoregions Western European Broadleaf Forests (Olson *et al.* 2001) and to the Central Highlands (based on aquatic fauna, (EEA 2014). However, in my thesis I combine them in the term ‘cultural landscape’.

Types of landscape: The study sites of Fichtelgebirge and Frankenalb are characterized by agricultural land use, whereas Grafenwöhr is used for military training.

Semi-natural areas are partly found in agricultural landscapes in form of hedges, transition zones, grasslands or pastures with low-intensity impacts (e.g., Hietala-Koivu *et al.* 2004; EFNCP 2014). But at Grafenwöhr Training Area, most of the site is maintained in a natural to semi-natural state with partly no impact at all (e.g. wetlands, some forested parts) or only very basic mowing or tree removal. Therefore, in my thesis I refer the term “semi-natural landscape” exclusively to Grafenwöhr Training Area and ‘agricultural landscape’ to Fichtelgebirge and Frankenalb.

Chapter 2

2 EFFECTS OF MILITARY DISTURBANCES ON PHYTODIVERSITY AT GRAFENWÖHR TRAINING AREA

2.1 INTRODUCTION

Military training areas are typical landscapes that combine heavily disturbed with nearly untouched areas. They are commonly seen with mixed emotions because they often conjure images of demolition and destruction (Coates *et al.* 2011). This presumption is compounded by the fact that access to such areas is very limited. Without a doubt, military training has a substantial impact on landscapes. Several studies on active and former military training areas have been conducted, mostly in relation to tank driving (e.g., Shaw & Diersing 1989; Ayers 1994; Prosser *et al.* 2000; Haugen *et al.* 2003; Li *et al.* 2007b) and fire (e.g., Diersing *et al.* 1992). Most obvious disturbances are the visible effects on the vegetation (injury, mortality) and increasing soil erosion after the removal of the vegetation cover (Milchunas *et al.* 1999; Graham *et al.* 2009). Johnson (1982), for example, reports a bisection of vegetation cover after some years of tank training. Topsoil removal influences abiotic (soil resources) and biotic (competition) conditions (Jentsch *et al.* 2009). These damages and destructions predominantly arise through tank driving, and digging of anti-tank ditches, emplacements and foxholes (Warren & Herl 2005), but also due to bivouacking (Trame 1997).

Indirect effects, caused by driving with heavy wheeled of tracked vehicles, are the changed physical characteristics, like soil water, root penetration, reduced pore size, and seedling establishment that also might change competition (Goran *et al.* 1983; Alakukku & Elonen 1995; Milchunas *et al.* 1999; Perkins *et al.* 2007; Wu *et al.* 2008). Silveira *et al.* (2010) report a change in bioavailability of carbon and a different C:N ratio after disturbance.

These changes appear after a time-shift in the composition of plant species. Several studies report a replacement of large perennial species by smaller annual plant species (e.g., Rowlands 1980; Severinghaus e*t al.* 1981; Hirst *et al.* 2003) and the reduction of above ground biomass (Hall 1980). Dickson *et al.* (2008) discovered a reduced change of vegetation in these plots with a higher amount of native (prairie) species than alien C3 grasses. Furthermore, tank driving increases the distances between plant species individuals (Palazzo *et al.* 2005).

Direct but not visible influences are the subsoil compaction (up to depths >50 cm - Prosser *et al.* 2000), which are still evident more than 40 years after disturbance (Shaw & Diersing 1989). The degree of these disturbances depends on the soil type (Hirst *et al.* 2003; Caldwell *et al.* 2006), its humidity (Payne *et al.* 1983; Dickson *et al.* 2008), the way the vehicle was passing (straight in line or turning - Shaw & Diersing 1989) and the weight of the vehicle (Voorhees *et al.* 1986).

In a study of Haugen *et al.* (2003), the researchers criticized the usually randomized sampling without being able to distinguish the real impact of a tank in a maneuver. They equipped a tank with GPS and found that during 16% of the off-road time a tank has a significant impact on the vegetation, especially in turning. An average width of vegetation removal of 14 cm per driven meter sums to an average of more than 5600 m^2 per tank mission. However, from an ecological point of view, these impacts, or disturbances, create new opportunities for species succession and compe¬tition. Disturbance is an integral component of landscape ecology, a natural and ongoing occurrence, which can be easily overlooked (Warren *et al.* 2007).

Several studies proof the high environmental value of military training areas. Gazenbeek (2006) promotes the "spectacular amounts of natural and semi-natural habitats". The Deutscher Rat für Landespflege (1993) justifies the high species numbers with the complex landscape with recurring incipiency. Warren & Büttner (2008b, 2014) found evidence for the correlation between high numbers of endangered amphibians and the disturbances on military training areas. Cizek *et al.* (2013) recorded more endangered butterflies on military training areas in Czech Republic than in nature reserves but sees no effect for vascular plants. Maneuvers are planned and performed in units. Due to tactical reasons, some areas might be utilized more frequently than others (Milchunas *et al.* 2000) or occupy more space because of men and machinery (Demarais *et al.* 1999), and therefore are more burdened. Since training has to be as realistic as possible, it occurs in all weather conditions and around the year. There is not much space to consider environmental damages, with high damages on wet and less damage on dry soil (Fehmi *et al.* 2001). These disturbances create heterogeneous patterns, with turned soil like on plowed fields (Fehmi *et al.* 2001) and untouched vegetation right next to it and therefore offer niches for numerous species of flora and fauna.

Homogeneous landscapes support only an established species pool and provide little chance for rare vegetation species to settle and proliferate, even if they are already present in the seed bank of the soil. This is also the case for over-protected areas, such as undisturbed parks or abandoned military training areas that lose their open character due to succession because of the missing disturbance (Gaertner *et al.* 2010).

The species established in these static systems limit the resources available for others that are not as adapted to the environmental conditions. The germination of lesser-adapted species is often hindered by the need for exposed soil or soil turnover, resulting in competitive exclusion.

Evidence suggests that natural and anthropogenic disturbances interact in many ways and that regional biodiversity is maximized by this interaction (White & Jentsch 2001). In other words: species are disturbance-dependent (Hunter *et al.* 2001).

Warren *et al.* (2007) compared areas administered by the six largest U.S. federal land management agencies (Fig.): the Bureau of Land Management (BLM), the Forest Service (FS), the Fish and Wildlife Service (FWS), the National Park Service (NPS), the Bureau of Indian Affairs (BIA) and the Department of Defense (DOD). Both the species richness and density were shown to be greater on military land (DOD) (Figure 2-1).

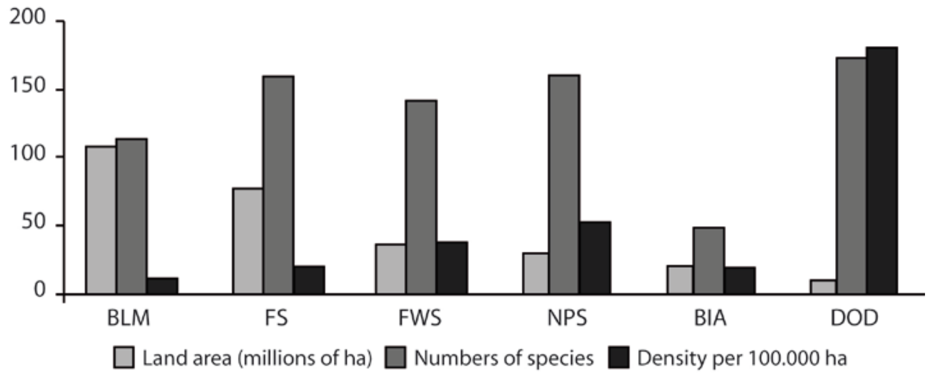


Figure 2-1: A comparison of size, species richness and density in 1992 on land administrated by the six largest U.S. federal land management agencies (BLM = Bureau of Land Management, FS = Forest Service, FWS = Fish and Wildlife Service, NPS = National Park Service, BIA = Bureau of Indian Affairs, DOD = Department of Defense). Source: Warren *et al.* 2007.

Today, active and former military training areas are of high nature value (Deutscher Rat für Landespflege 1993; Gaertner *et al.* 2010). The extensive land-use on large scale, the absence of fertilizers, and the open and mostly unfragmented landscape are refugia for endangered plants and animals (IUCN 1996; Naturstiftung David 2007). On the two training areas within Bavaria we find one third of all vascular plants of the whole State of Bavaria (Naturstiftung David 2007). Therefore more and more areas with (formerly) military use are put under the umbrella of the Natura-2000 network (Gazenbeek 2006).

All these studies indicate that military training areas are well suited for research in the field of disturbances and species richness. But these studies are subject to a single sided view. Most studies consider just one disturbance type. But overlapping disturbances, like the anthropogenic military use and natural disturbances, like damages caused by wild boar can occur on the same spot. Furthermore, most studies lack proof of landscape heterogeneity and patch diversity.

QUESTIONS & HYPOTHESES

As described, it is expected Grafenwöhr Training Area to be very species rich. The question is what influences the species richness in detail. Is it an overall heterogeneity of the landscape, as stated in the heterogeneous disturbance hypothesis (Warren *et al.* 2007), or rather single land-use practices? Are there certain disturbances or frequencies responsible for the diversity of plants and how much do combinations of different parameters explain species richness?

Therefore I state the following hypotheses:

- H1) The military training area shows a high diversity of land uses and disturbances, which leads to a heterogeneous landscape.
- H2) The heterogeneity of land uses and overlapping disturbances increases species richness.
- H3) Species richness cannot be related to a certain land-use type and disturbance.
- H4) The open landscape shows a high similarity between patches, because the nearly unrestricted off-road driving enhances seed distribution.
- H5) Threatened and endangered species are mostly found in the moderately disturbed open landscape.

2.2 STUDY SITE

Grafenwöhr Training Area is located between the name giving town of Grafenwöhr to the east, Auerbach in der Oberpfalz to the west and Vilseck to the south in the administrative district of Upper Palatinate (Oberpfalz) about 90 km northeast of Nürnberg.

Two natural regions converge in the study area (Figure 2-2): Franconian Jurassic (Fränkische Alb) and Upper Palatine Hills (Oberpfälzisch-Obermainisches Hügelland) (Ssymank 1994), which are separated by the Freihung fault zone (Warren & Büttner 2006). Corresponding to this area are the ordinance survey maps no 6236/3 and no 6336/1 in scale 1:25000.

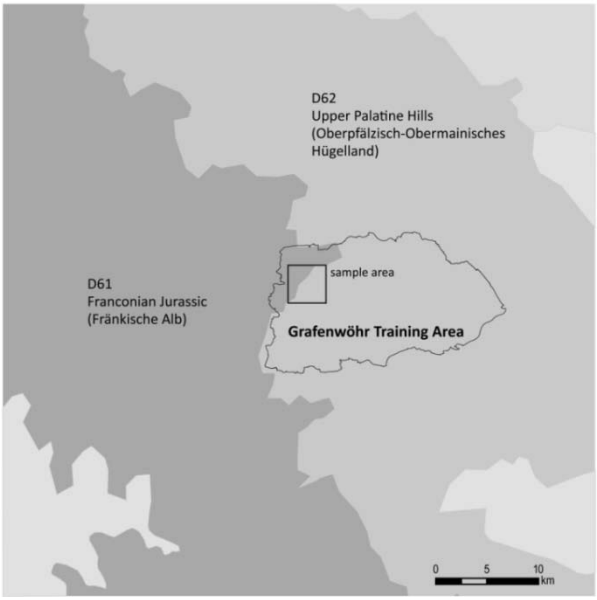


Figure 2-2: Converging natural regions within the survey area. Main units after (Ssymank 1994).

These regions are characterized by relatively homogeneous geology, climate and morphology. The eastern part of the training area is characterized by Triassic sandstone and sandy soils, whereas the western part of the area, where the survey plots were placed, mostly Late Jurassic sediments of lime and dolomite are found, covered by dry Cretaceous sands (Figure 2-3). Keuper and Lias may be found in areas where ridges cut through the relief. At some locations, such as Rattenleite, spring horizons resulting from ground-water retaining clay horizons can be found (Figure 2-4). Average annual precipitation is approximately 740 mm, and mean annual temperature is 7.3 ° C (Climate Stations Grafenwöhr and Eschenbach, German Weather Service).

Figure 2-3: Dry sand grassland with typical plant species: *Artemisia campestris*, *Dianthus deltoides*, *Holcus lanatus*, *Jasione montana*, *Koeleria pyramiddata*, *Thymus pulegoides* and *Trifolium arvense*.

Figure 2-4: Spring horizon with typical plant species: *Blechnum spicant* and *Equisetum sylvaticum*.

Grafenwöhr Training Area (GW) is approximately 23,000 ha in size (Burckhardt 1994; Warren & Büttner 2008a). The training area was established in 1907 for the III Corps of the Royal Bavarian Army and expanded in size in 1936. In 1945 the 11th Armored Division, Third U.S. Army occupied the training area (Burckhardt 1994). For the initial establishment of 90 km² area ten small villages and hamlets with 240 inhabitants needed to be evacuated, which was completed in 1910. The expansion to 226 km² needed to be done because of the growing Wehrmacht and the longer range of the modern guns. For this another 1500 people from 57 villages, hamlets and isolated farms needed to be resettled (Burckhardt 1994). The remains of these settlements are still visible by walls, cellars, the churches of Hopfenohe and Pappenberg, and several cemeteries. At present it is used for qualification and training, especially for armor, infantry and aviation weapons (Warren & Büttner 2006). There are two ways in conducting these trainings. These are either at static installations, like fire-ranges, or from moving vehicles on specially built multi-purpose range complexes like Range 301. In the late 1980s, a live-fire area of approximately 2,500 ha was established. It is used for cross-country maneuvers for whole companies and includes an impact area for live fire in the center of the training area (Warren & Büttner 2006). Since 2006 Grafenwöhr Training Area houses the 7th Army Joint Multinational Training Command (JMTC) but is also used by other international NATO troops.

2.2.1 Sampling methods

Field work was conducted from May to August 2008 at the Grafenwöhr Training Area (GW). Data sampling took place in the western part of the training area in a 16 km² section, ranging in elevation from 440 m to 560 m ASL. Field work was conducted by me and Alexander Ulmer (botanist), with some support of Daniel Hornstein and Daniel Thiel.

On a topographic map, scale 1:25,000 (Amt für Geoinformationswesen der Bundeswehr, 100th ASG GW Range Operations) a systematic survey grid with quadratic shape of 4 km x 4 km was placed, using Arc GIS 9.3 (ESRI Inc. 1999-2008) software. One hundred plots, each with a size of one hectare (100 m x 100 m), were placed regularly within the survey grid, each separated by a distance of 400 m. The grid was orientated northwards in order to identify the edges easily (Figure 2-5Figure 2-5). The positioning of the grid was limited by access restrictions at Impact Area B and the two overlapping quarries where entry was prohibited out of secrecy and safety reasons. It was also important to position the grid such that both forest and grassland were sampled. Field work was conducted in close coordination with Range Security to avoid areas with ongoing training and the Environmental Division of Grafenwöhr Training Area. A random sampling of the one hundred plots was quasi given since the active military training schedule allowed only access to a few plots in the same time.

Collecting soil samples was not possible because of partly non visible non explosive munitions (duds) in the ground which would have implicated additional man power from the Range Security for clearance.

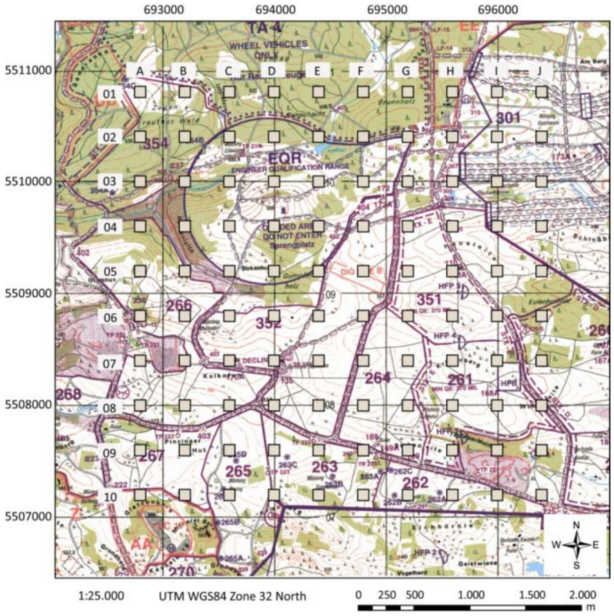


Figure 2-5: Distribution of the 100 plots (1 ha each) within the survey grid, placed on TK25.

For characterizing the influencing disturbance variables an identification key for land use and disturbances in cultural landscapes (Buhk *et al.* 2007) was adapted (Table 2-1). This key, actually a check list, contained information about land use, disturbance types and temporal (frequency, seasonality, duration) and spatial (size, form, distribution) characteristics of these disturbances, and furthermore information about the selectivity of a disturbance.

To include disturbances caused by military training activities, this classification key was expanded. An initial literature review of the influence of military disturbances indicated a variety of potentially interacting impacts resulting from military training activities. Disturbances directly caused by military actions include compaction and damage to vegetation and soil from trampling by foot traffic (Whitecotton *et al.* 2000), wheeled vehicles (e.g., Hernando 1999; Perez 1999) and tracked vehicles (e.g., Wilson 1988; Milchunas *et al.* 2000; Prosser *et al.* 2000; Garten & Ashwood 2004; Leis *et al.* 2005; Wu *et al.* 2008; Silveira *et al.* 2010; Ödman *et al.* 2012). Further disturbances in scientific literature were bivouacking (Trumbull *et al.* 1994), excavations in different sizes, from small foxholes to excavations for weapon system emplacements, antitank ditches and constructions (Warren & Herl 2005).

Indirect disturbances were leveling processes on the digging sites, graveled roads (mostly made of lime stone), soil banks (berms) along the roads to divert military traffic (Warren & Herl 2005) and for tactical training, and fire (accidental during shooting or prescribed for maintenance reasons (Diersing *et al.* 1992; Quist *et al.* 2003; Wanner & Xylander 2003).

During the sampling process, additional observations in the field and information collected from Range Control and the forest official were recorded and attached to the key. The highest level of uniform disturbance was found in areas where leveling actions are performed and gravel applied. In some of these areas (especially Range 301), controlled burns were used to prevent succession.

Table 2-1: Land-use and disturbance classification key, that based on Buhk *et al.* 2007 and which was extended by land-use and disturbance types on Grafenwöhr Training Area.

LAND USE					
field	cereal stand	maize stand	root crop	rape	intermediate crop
path	footpath	field/forest road	asphalt road	gravel road	paved road
fallow land / succession	young (1-2 years)	intermediate	older stage (shrubs)	old (pre-forest stage)	complex
rock	not in use	rock climbing	quarry	stone wall / heap	
water body	running - regulated	running - natural	standing - artificial	standing - natural	spring
	trench	bayou			
transition zone	forest margin	field margin	meadow margin	road margin	hedge
	hedge with trees	gallery forest	single tree	grove	trench
	field bosk	bank			
grassland	meadow	pasture	soilage		
forest (>100sqm)	single tree felling	grove felling	clear felling	thinning	riparian forest
	breakage	clearance	tree nursery		
settlement	farm yard	military construc./bivouac	single house	sealing	deserted village
misc. construction	waste heap	bridge	retaining basin	torrent control	

DISTURBANCE TYPES					
none	clear felling	grove felling	single tree felling	thinning	removal of sead wood
wood storage/movement	skidding track	rejuvenation	breakage	seeding	biomass input
biomass output	compaction (trampling)	compaction (wheels)	compaction (tracks)	pond drainage	agricultural use
nutrient contamination	pesticides	mowing	microherbivory	macroherbivory	wild boar
varmint	flooding	farm	rock/soil movements	gravel (limestone)	gravel (basalt)
tramp material	quarry	hydraulic engineering	dehydration	erosion (water)	erosion (wind)
depression (water filled)	fire	contamination (oil, munition)	excavation (open)	excavation (filled)	trench (filled)
leveling	sealing	influence of salt	fencing		
DISTURBANCE CHARACTERISTICS					
frequency	every 100 years	every 10 years	annual	twice a year	3 times a year
	> 3 times a year	steady diffuse	steady intense		
seasonality	1st quarter	1st + 4th quarter	1st - 3rd quarter	1st - 4th quarter	2nd quarter
	2nd - 3rd quarter	2nd - 4th quarter	3rd quarter	3rd - 4th quarter	4th quarter
duration	< 1day	< 1 week	< 1 month	< 1 year	> 1 year
size	punctiform/ linear	1/4 of areal	1/2 of areal	3/4 of areal	complete areal
form	linear	laminar	punctiform		
distribution	homogeneous	heterogeneous			
selectivity	none	age	species	location	land parcel boundary

Plots were divided up into patches with different land use types or patches with the same land use but different disturbance types (Figure 2-6). In rare cases of similarity within these two parameters, information regarding the temporal and spatial characteristics and / or selectivity of the disturbance were consulted. The standard procedure was to allocate a new patch if at least one parameter was different. The minimum area of a patch was defined as 10 m² and the minimum linear size as 1 m in width. It was assumed that there is no landscape without a disturbance. Time-related disturbance descriptors were used to explain disturbances in the past, e.g., clear-felling once in a century.

Figure 2-6: Example of a surveyed plot (G10) after subdividing the 1 hectare plot (black square) into eleven patches (numbers). Grid: UTM WGS84 Zone 32 North.

For each patch within a plot, the general characteristics were noted on a check list, and the different plant species were recorded. Therefore the dataset consists of both quantitative (species richness, coordinates) and qualitative data (characteristics). Furthermore, data were collected regarding the selectivity of the disturbance in relation to the plant age, species type, and the location of the disturbance. For this data set also combinations of different selectivity were recorded (e.g., the age and the species of a tree for selective tree cutting).

In cases where multiple disturbances or several types of disturbance with similar effects were recorded within one patch (e.g., compaction by foot traffic or vehicular use), differentiation was needed to distinguish between influences of military, nature, or maintenance (for an example see Table 2-2). Even if one disturbance type resulted from the other one (e.g., mowing and compaction by the wheels of the mowing machine), at least in this case the form and distribution of the disturbances were different.

Table 2-2: Example of differentiation between disturbances in patches. Disturbance types are characterized in more detail using frequency, size, form and distribution of the disturbance.

plot	**patch**	**land use**	**disturbance type**	**frequency**	**size**	**form**	**distribution**
A02	A02-01	grassland	mowing	annual	4/4 area	areal	homogeneous
A02	A02-01	grassland	compaction (wheels)	annual	linear/punctif.	linear	heterogeneous

Identification and labeling of plant species was done after the nomenclature of Jäger *et al.* (2005) and Möhl & Eggenberg (2007). Species names were verified according to the databases FloraWeb (Bundesamt für Naturschutz - www.floraweb.de) and BiolFlor (Klotz *et al.* 2002). Threatened and endangered species were classified according the Bavarian Red List (LfU 2002; STMUG 2005) and FloraWeb. All data were put into an Access 2007 database.

2.2.2 Land-use types at Grafenwöhr Training Area

The patches within the survey plots were allocated to eight different land use types: ‘grassland’, ‘forest’, ‘fallow land’, ‘path’, ‘transition zone’ (boundary), ‘water body’, ‘settlement’, and ‘miscellaneous constructions’. Figure 2-7 shows the land use types associated with each survey plot. The three dominant land use types are indicated in green (forest), yellow (grassland) and brown (fallow land). While forests are primarily located in the northwestern part of the survey area, grassland areas concentrated in the center and southern part. Fallow land is not clustered in any particular section of the survey area.

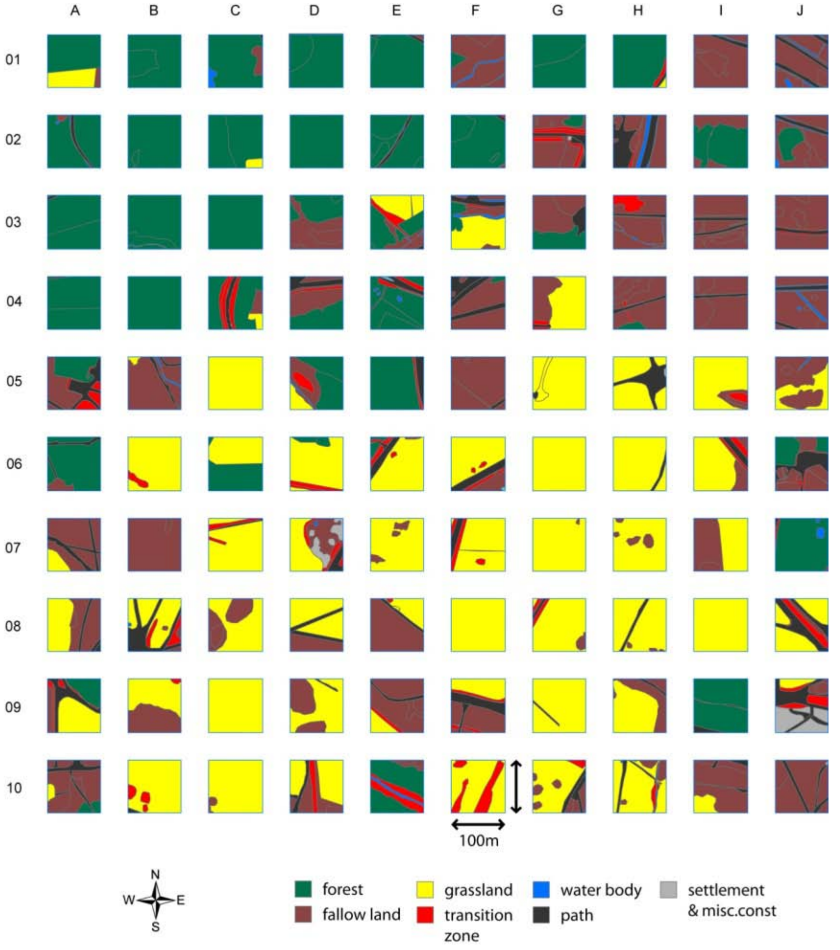


Figure 2-7: Land use types classified within the survey area. Each box represents an one-hectare plot. Interspaces between plots were reduced for display.

Nearly 90% of the area is classified as 'grassland', 'forest' or 'fallow land'. 'Paths', representing gravelled areas like roads, in addition to plains, and boundaries sum up to ten percent of the area whereas the remaining categories 'water body' and 'settlement & miscellaneous constructions' (e.g., guard houses) barely cover one percent (Table 2-3).

Table 2-3: Breakdown of the area surveyed based on land use type, and the number of patches where land use type occurs.

Land use type	Total area [%]	Number of patches
Grassland	34.1%	78
Forest	27.6%	78
Fallow land	27.4%	198
Path	6.4%	96
Transition zone	3.3%	95
Water body	0.7%	39
Settlement & misc. constructions	0.5%	11

The size of the area covered by different land use types gives further information about the characteristics of these classes (Figure 2-8). ‘Grassland’ is the land use type with the largest homogenous area, covering an average of 4,300 m² per plot. Plots with this land use type are concentrated in the center and southern part of the survey area and are characterized by a mowing regime (Figure 2-7). These areas are widely used for training activities using tanks. With an average of more than 3,500 m² per plot, ‘forests’ follow. These areas mostly situated in the northwestern part of the survey area and predominantly used for forestry. Also common in the survey area, ‘fallow land’ is subject to succession and is not explicitly characterized by a disturbance regime. The remaining four classes are relatively seldom. ‘Paths’ combine roads and gravelled areas, mostly consisting of limestone and used for infrastructure. Besides the gravelled areas, they are mostly in a linear shape. Combined in a class with other man-made structures (e.g., drainage ditches), ruins of abandoned settlements are not uniformly distributed across the area. The ’transition zones’ (or ‘boundaries’) classification includes areas that form an intermediate strip between two different disturbed areas. For example, areas such as marginal strips along gravel roads and transition zones between forest and open grassland belong to this class. Boundaries are generally linear in shape. The last land use type consists of ‘water bodies’. They are mostly square in shape and are located within areas where tank training is conducted and often originate from excavations for tanks.

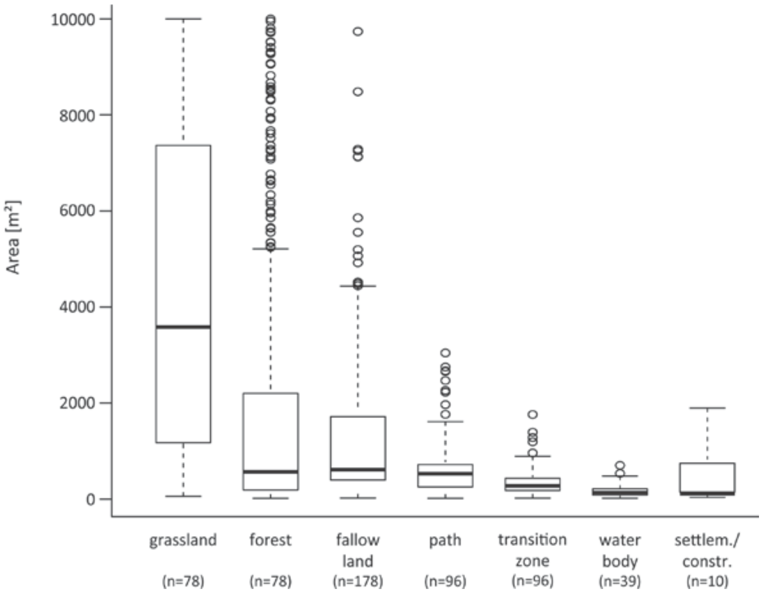


Figure 2-8: Mean size of the different land use types in m² and number of patches of occurrence (n_{max} = 595 patches).

2.2.3 Disturbance types at Grafenwöhr Training Area

At Grafenwöhr Training Area, 35 disturbance types were recorded within 595 patches. The by far most frequent disturbance was the compaction by wheeled vehicles on 52% of all patches, followed by compaction of tracked vehicles (34%, Figure 2-9) and macroherbivory (32%). Herbivores' impacts were observed at bushes (gnawed buds), trails and resting places and is also recorded in compaction by trampling if significant in size. Foreign materials (all materials that do not origin from the place where they were recorded) and limestone gravel are also among the six most frequent disturbance types. They sum up to 147 patches, and include, for example, gravel on the roads and banks along the roads with a core of stones and gravel (Figure 2-10).

Figure 2-9: Trace of a tank track.

Figure 2-10: Bank at Grafenwöhr Training Area. They were situated next to roads and mostly consisted of a gravelled core, covered with soil. They are used for tactical training and to protect from lime dust.

In focusing the plot scale, we recorded wheeled vehicles on nearly every plot. They do not necessarily be related to military training, but also to maintenance actions, like mowing and works in the forests. Three quarter of plots showed traces of macroherbivory, whereas on two of three plots tracks and foreign material were found (Table 2-4). Similar results were found on patch scale (Figure 2-11).

Table 2-4: List of disturbance types that were recorded on at least 20% of the 100 plots of Grafenwöhr Training Area.

Disturbance type	**Occurrence [%]**
Compaction by wheeled vehicles	96
Macroherbivory	75
Compaction by tracked vehicles	66
Foreign materials	65
Mowing	61
Limestone - gravel	59
Compaction by trampling	43
Single tree felling	36
Water filled depressions	22

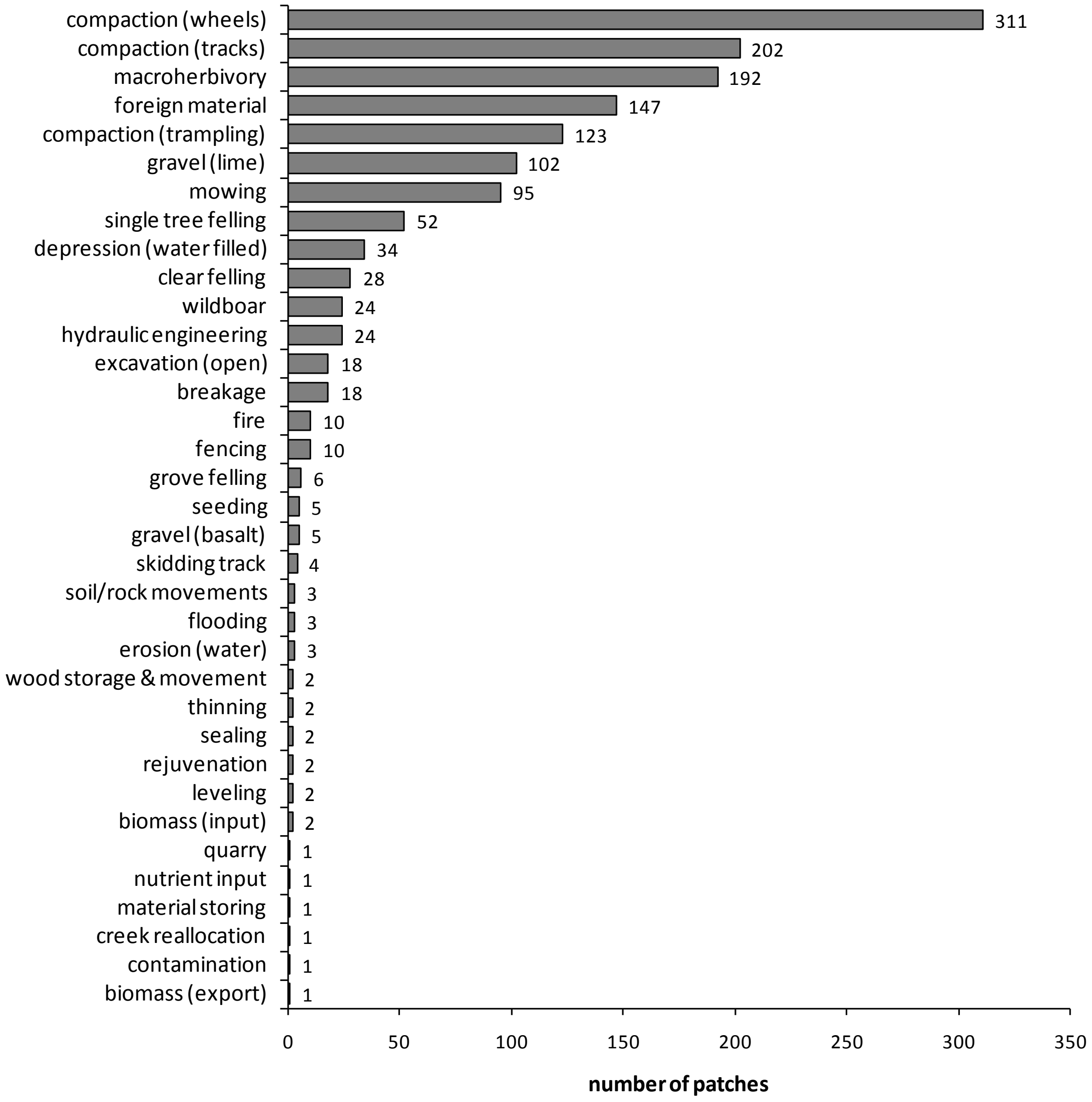


Figure 2-11: Disturbance types and their occurrence on 595 allocated patches. Most patches were disturbed by wheeled and tracked vehicles and by macroherbivors.

2.3 STATISTICAL METHODS

Partial Least Squares Regression and Boosted Regression Trees were carried out to analyze the influence of the multiple variables on plant species richness and to filter and reduce the number of variables to the significant ones.

Partial least squares regression (PLS-R) was originally introduced by H. Wold as a method for relating two data matrices (Wold 1975). This method combines features from principal component analysis (PCA) and multiple regressions. PCA transfers the variance of a multivariate dataset to reduced principal components. This process avoids multicollinearity, a situation where two or more variables are highly correlated, which affects the calculation of the individual predictors. A big advantage of this method is the possibility to use both qualitative and quantitative data in the creation of regression equations. PLS-R was used in concordance to Buhk *et al*. (2007b), to describe and analyze the relationship between plant species richness within each plot (alpha diversity) and the land use or disturbance descriptors. An optimization is possible using the jack-knifing procedure (Quenouille 1949; Tukey 1958 in Miller 1974) that resamples in leaving out one or more observations at a time from the dataset. Two approaches were conducted. (1) A partial least squares regression and one further calculation with the significant parameters and (2) several regressions to reduce the parameters to a minimum number without to provoke a breakdown of the model according to Buhk *et al.* (2007b).

For conducting PLS-R the software The Unscrambler version X 10.1 (CAMO 2010) was used. All values were standardized (A/(SDev + B) and significance was determined by uncertainty test with full cross-validated before the analyses.

Boosted Regression Trees (BRT) is a further technique that combines algorithms and therefore improves the performance of a single model (Elith *et al.* 2008; Elith & Leathwick 2013). It uses a combination of regression trees and boosting. Regression or decision trees relate a response to their predictors by recursive binary splits (De'ath & Fabricius 2000; De'ath 2002, 2007; Moisen 2008), whereas boosting combines many simple models, resulting in improved predictive performance (Elith *et al*. 2008). The advantage of BRT is that quantitative and qualitative variables can be described without excluding outliers. Furthermore, this type of analysis considers interaction effects between predictors and offers results in terms of percent of the variation of species richness described by each variable.

For conducting Boosted Regression Trees the open source software R version 2.15.3 (R Core Team 2013) with packages ‘gbm’, version 2.1 (Ridgeway 2013) and ‘dismo’, version 0.8-17 (Hijmans *et al.* 2013) was used.

In the package gbm there are several functions to be adjusted to the certain data set. The tool “bag fraction” specifies the proportion of data to be selected at each step (Elith *et al.* 2008). A “learning rate" regulates the contribution of trees required for analysis. The estimation of optimal adjustment is reached with cross validation (deviance reduction). A simplification, the dropping of unimportant variables, is possible due to the results of a 10-fold cross validation (cv) procedure (see Elith *et al.* 2008).

Analyses were conducted on plot (landscape) and patch (local) level. Correspondingly, data slightly differed on these two scales. Whereas at larger scale, the heterogeneity of the plot was included, fuzzy variables were calculated that counted the number of different parameters within a plot, i.e. land use, patch numbers, disturbance types, frequencies, etc. These variables were named 'number of different land-use classes (per plot)', 'number of different disturbance-types', etc. (Table 2-5).

Table 2-5: Table of parameters for multivariate statistics on plot (landscape) level.

Category	**Variables**
General information:	species richness/patch
Fuzzy variables:	number of patches per plot; number of different land uses per plot; number of different disturbance types per plot; number of different frequencies per plot; number of different seasons per plot; number of different durations per plot; number of different sizes per plot; number of different forms per plot; number of different distributions per plot; number of different selectivities per plot
Land uses (1/0):	forest; miscellaneous constructions; field; path; rock; settlement; transition zone; water body; fallow land/succession; grassland
Disturbances (1/0):	agriculture; biomass export; biomass input; breakage; clear felling; compaction (tracks); compaction (trampling); compaction (wheels); contamination; creek reallocation; collecting deadwood; dehydration; depression (water filled); erosion (water); excavation (open); farming; fencing; gardening; fire; flooding; foreign material; gravel (basalt); gravel (lime); grove felling; hydraulic engineering; leveling; macroherbivory; material storing; macroherbivory; mowing; none; nutrient input; pesticides; pond-drainage; quarry; rejuvenation; sealing; seeding; single tree felling; skidding track; soil/rock movements; thinning; wild boar; wood storage/movement
Frequencies (1/0):	1x/century; 1x/decade; 1x/year; 2x/year; 3x/year; >3x/year; steady diffuse; steady intense; none
Seasonalities (1/0):	quarter 1; quarter 1-3; quarter 1-4; quarter 1&4; quarter 2; quarter 2 & 3; quarter 2-4; quarter 3; quarter 3 & 4; quarter 4; none
Durations (1/0):	<1day; <1week; <1month; <1year; >1year; none
Sizes (1/0):	1/2-area; 1/4-area; 3/4-area; 4/4-area; linear/punctiform; none
Forms (1/0):	laminar; linear; punctual; none
Distributions (1/0):	heterogeneous; homogeneous; none
Selectivities (1/0):	age; location; species; age & location; age & species; age & species & location; species & location; lot-boundary; none

For analyses with different portions of forest cover on landscape level the 595 patches were allocated to forest or open landscape according their land-use. With ArcGIS (ESRI Inc. 1999-2008) area was calculated for each patch and summarized for each plot. To figure out the differences between the different proportions of forest cover, the following categories were calculated: 0-5%; 0-25%; 0-50%; 51-100%; 76-100%; 96-100%.

2.3.1 Ellenberg indicator values for analyses on patch level

For the analyses on patch (local) level, information about abiotic factors were included. Since soil samples were not available, Ellenberg indicator values for plant species were used instead (Ellenberg 1991). They were derived from the databases BiolFlor (Version 1.1 - Klotz *et al.* 2002) and LEDA (Kleyer *et al.* 2008).

The parameters 'median', 'maximum', and 'minimum' were calculated for the Ellenberg values L (light), T (temperature), K (continentality), F (soil moisture), R (pH), N (nutrients/nitrogen), and S (salinity). These variables were included as: L.min; L.med; L.max; T.min; T.med; T.max; K.min; K.med; K.max; F.min; F.med; F.max; R.min; R.med; R.max; N.min; N.med; N.max; S.min; S.med; S.max.

2.3.2 Beta diversity

To analyze beta diversity of the vegetation (similarity of species composition) the Sørensen similarity index for presence-absence data was calculated for all pairs of plots. The Sørensen index performs well in different studies and evaluations (Koleff *et al.* 2003). Standard deviation of the Sørensen index was calculated to assess within-landscape heterogeneity (Jurasinski & Kreyling 2007). Between-landscape similarity was assessed by treating each landscape as a single relevé of presence/absence data and computing Sørensen similarity. Plots were then correlated using Spearman ρ correlation. Significance was determined using Mantel tests (1000 iterations). Kriging was conducted using ArcMap 9.3 (ESRI Inc. 1999-2008).

2.4 RESULTS

2.4.1 Land use and disturbances on plot scale

2.4.1.1 Land use and species richness

Total plant species richness within the 100 sampled plots at Grafenwöhr Training area was 647. On plot scale a minimum of 66 plant species and a maximum of 298 plant species were recorded, with a mean of 148.3. Most species were found on fallow land, consisting of nearly 82% of all recorded species within the survey plots. The diversity of forests showed an unexpected high species richness with a total number of 489 different plant species. Lowest diversity was recorded in the category 'settlement & miscellaneous constructions', with 240 species (37% of all recorded species).

For each land-use type, minimum, maximum and mean species richness were calculated from the data derived of the patches (α-diversity). Species numbers were highest in forest patches. Grasslands and fallow land showed a similar mean α-diversity. However, total species richness was significantly higher on fallow land (Table 2-6). Lowest mean species numbers were found on paths (mostly gravelled roads) and at water bodies. However, total richness was in the range of grassland patches.

Table 2-6: Land-use types of GW and related mean, minimum and maximum species richness (SR).

Land-use type	SR mean	SR min	SR max	Total species number	Land cover [%]
Fallow land	70	28	154	529	27.4
Forest	85	32	178	489	27.6
Transition zone	60	29	119	423	3.3
Path	57	20	134	376	6.4
Grassland	71	18	124	349	34.1
Water body	54	22	101	345	0.7
Settlement & misc. construction	66	23	98	240	0.5

An index for heterogeneity on plot scale was included in adding the patches with different land-use types within one plot. A linear regression confirmed the highly significant influence of the number of land use types on plant species richness (Figure 2-12). However, this analysis considered only different land-use types within a plot. Identical types were excluded. A regression, including the number of allocated patches, resulted in a highly significant relationship (Figure 2-13). The higher the number of patches (another expression for the heterogeneity of a site), the higher is the plant diversity. The plot with the maximum number of recorded plant species (J06: 298 species) contained 16 patches, and the plot with the minimum number of species (C05: 66 species) consisted of just one patch.

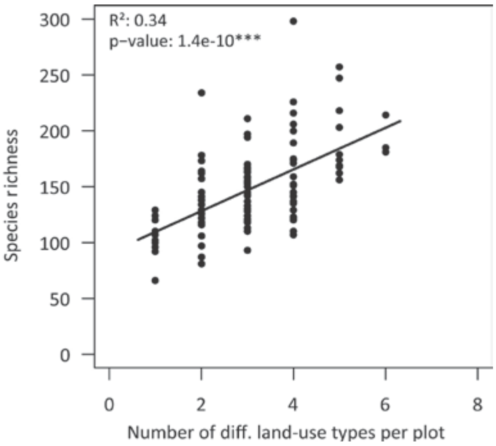


Figure 2-12: Linear regression of the relationship between the number of different land use classes per plot and species richness. The coefficient of determination of 34% and the high significance indicate that the number of patches is strongly correlated.

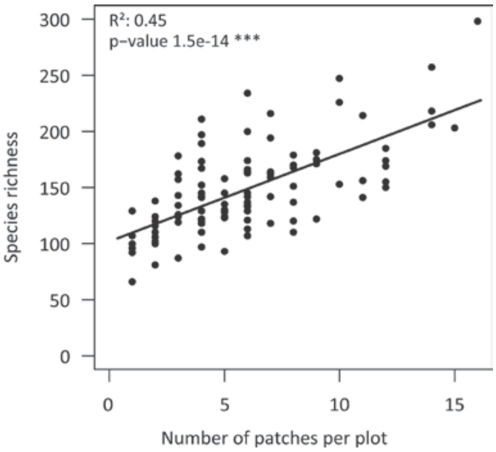


Figure 2-13: Linear regression of the relationship between number of patches per plot and species richness. The coefficient of determination of 45 % and the high significance indicate that the number of patches is strongly correlated.

The following figure (Figure 2-14) gives evidence for the heterogeneity of the landscape, showing a spatial representation of the species richness (α-diversity) in relation to patch number. Each plot is designated using circles with the diameter that increases with an increasing number of patches, illustrating the heterogeneity within a single sample unit. Noteworthy is the fact that the plots with the highest species richness (E04, J06) are not characterized by the highest number of patches.

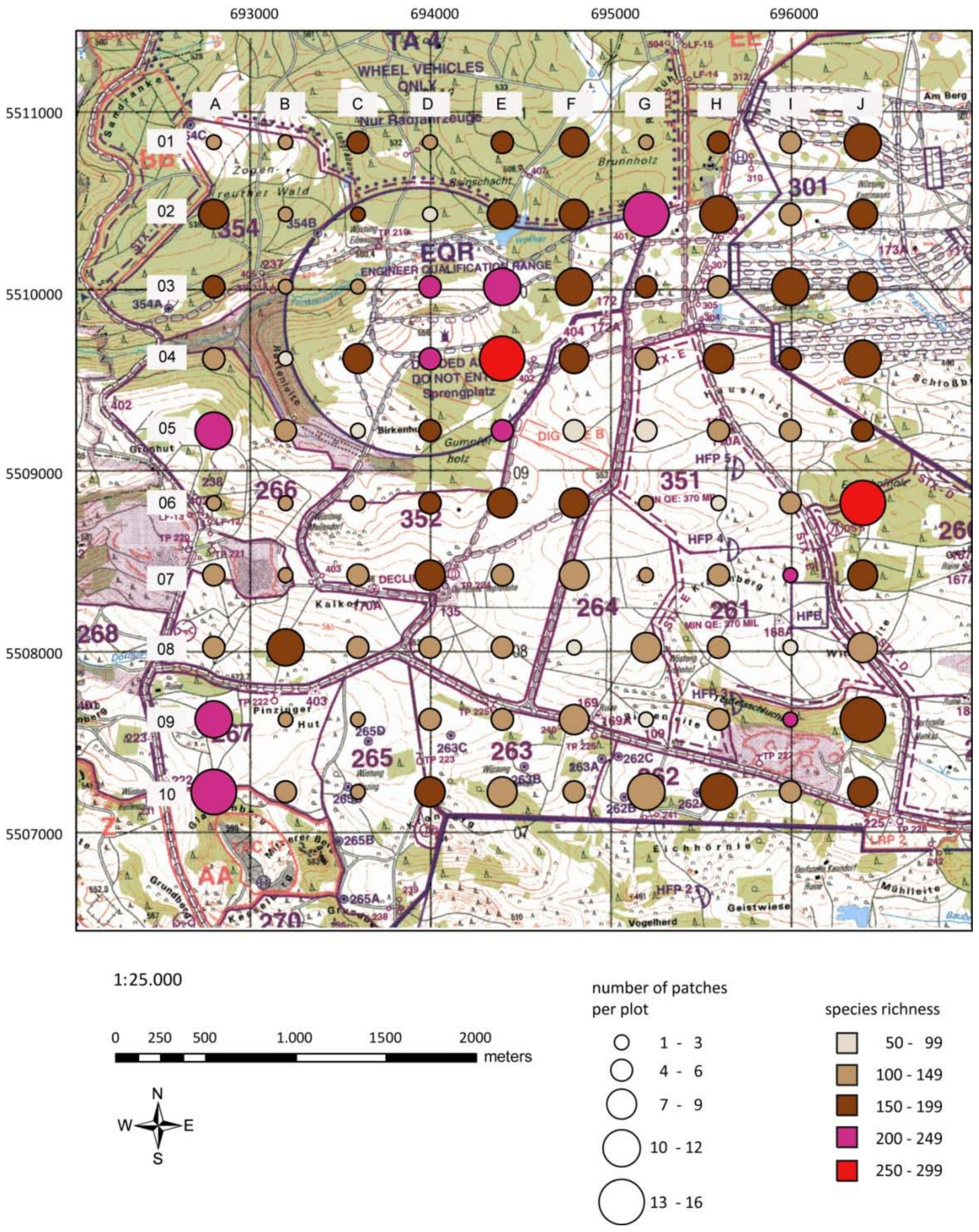


Figure 2-14: Alpha diversity in relation to the number of patches per plot. Circle sizes show number of assigned patches per plot from one (smallest) to 16 (biggest), colors display the recorded species richness from 66 (grey) to 298 (red).

2.4.2 Disturbances and species richness

In total, 35 different types of disturbance were recorded. A first figure should give an impression of correlations (Figure 2-15). Highest mean species richness is found on forested patches that are subject to grove felling and skidding tracks. But also disturbed areas by wild boar and the removal of single trees show not only a high mean richness, but also a broad variance of plant species richness. Lowest species numbers were found on sealed grounds or areas subject to rejuvenation.

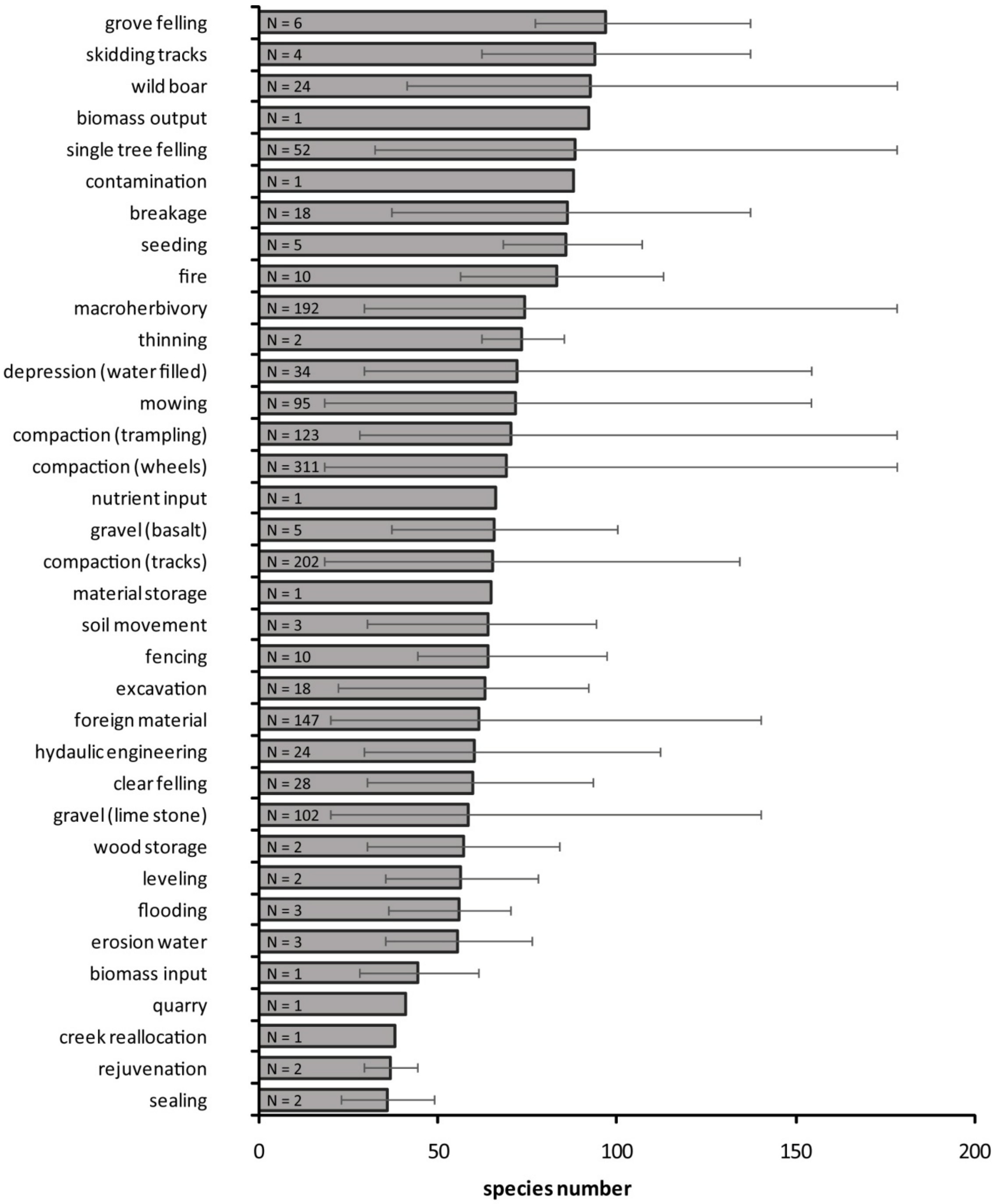


Figure 2-15: Minimum, maximum, and mean plant species number in combination with recorded disturbance types.

Similar to the heterogeneity of land-use types and numbers of patches on plot level, the number of disturbances was plotted with species richness, which resulted in a significant correlation as well. The higher the number of disturbances per plot, the higher is the biodiversity (Figure 2-16).

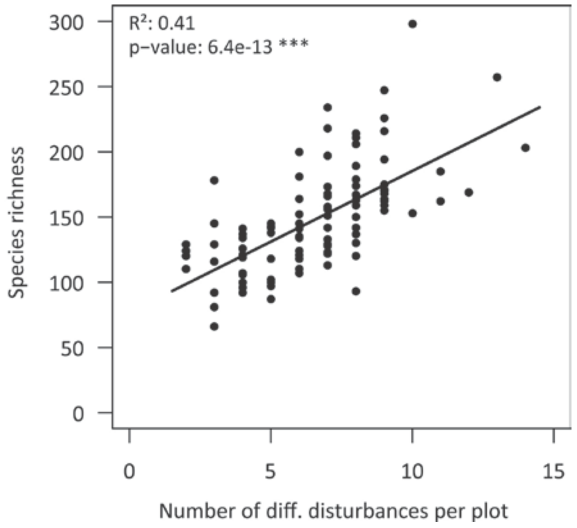


Figure 2-16: Linear regression of the relationship between the number of disturbance types per plot and species richness. The coefficient of determination of 41% and the high significance indicate that they are strongly correlated.

2.4.2.1 Influence of land use, disturbances and disturbance descriptors on species richness

Partial Least Squares Regression (PLS-R) on landscape scale was conducted with the 100 plots of Grafenwöhr Training Area. To explain species richness, a number of 112 variables were included (see methods Table 2-5). Mean species richness of all plots was 148.3. The regression shows a prediction of 61% (R^2=0.61) and a root mean square error (RMSE) of 25.8 (17.3%). The number of variables was reduced to 14 most significant ones (Table 2-7).

Table 2-7: Summary of results of Partial Squares Regression on full Grafenwöhr data on landscape level.

N	No. parameters	R²	RMSE	No. variables	No. significant variables	No. PLS-R axes
100	112	0.61	25.8	19	14	2

The X- and Y-Loadings of the PLS-R show ecologically highly connected variables related to forestry which are shown in the land-use itself, punctiform disturbances, single-tree felling, season 1 and 4 and the different selectivities (Figure 2-17). But also parameters indicating the heterogeneity of the disturbance regime (i.e. number of patches, number of different disturbance types and number of different seasons) were significant. Parameters of the first axis had an explanation power of 61%; further axes did not bring further achievements.

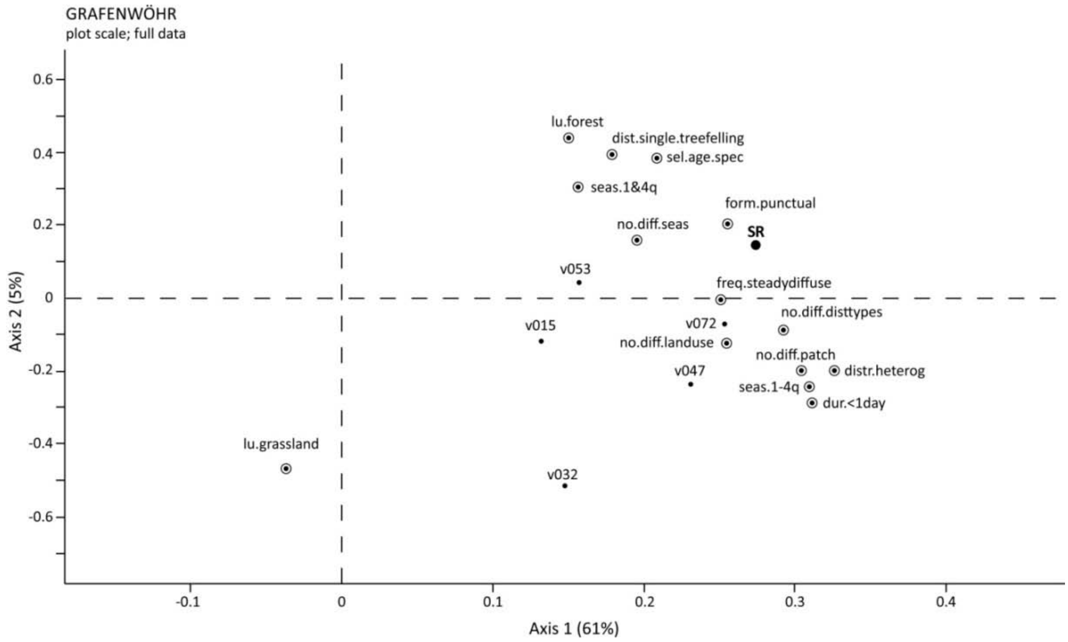


Figure 2-17: X- and Y-loadings of PLS-R on full Grafenwöhr data on landscape level. Parameters related to heterogeneity and forestry showed highest explanation. For description of variables see supplement S1.

A further analysis was conducted to force a reduction of parameters to a minimum without reducing the stability of prediction (see Buhk *et al*. 2007b), using several times the jack-knife function and selective deselection of parameters. Furthermore, analyses with Boosted Regression Trees (for method see chapter 2.3) were conducted to prove the results from PLS-R. Optimal adjustments are displayed in Table 2-8. A twofold simplification of the predictor set was conducted and reduced the number of important variables to 40 (Table 2-9).

Table 2-8: Results of adjustment of parameters for Boosted Regression Trees analysis on Grafenwöhr data after first (1) and second (2) simplification of variables. Grey fields show adjustable parameters.

	No. trees	**Tree complex.**	**Learning rate**	**Bag fraction**	**Est. cv deviance**	**Std. error est. cv deviance**	**Training data corr.**	**cv corr.**	**No of variables**
1	1250	5	0.01	0.5	4.45	0.35	0.97	0.77	76
2	1700	5	0.005	0.5	4.53	0.72	0.96	0.75	40

Table 2-9: Top 12 variables with highest explanation for species richness on landscape level, before and after predictors' reduction. Full results are displayed in digital supplement.

Top 12 predictors	before reduction (n=76) [%]	after reduction (n=40) [%]
No. of different disturbance types	12.1	12.2
No. of patches	11.9	10.7
Land use: forest	11.8	12.2
Form: punctual	6.8	5.9
Frequency: steady diffuse	5.9	4.7
Disturbance: macroherbivory	3.3	3.3
Distribution: heterogeneous	3.2	2.6
No. different selection	3.0	3.8
Season 1st & 4th quarter	2.8	3.2
Disturbance: foreign material	2.6	3.2
Selectivity: age & species	2.6	1.5
Season: 1st to 4th quarter	2.3	2.9

A direct comparison between the results of the methods PLS-R and BRT show the most important variables (Table 2-10).

Table 2-10: Comparison between results of analyses with the methods PLS-R and BRT. Six of ten predictors are consistent. Numbers in parentheses show BRT-ranking of significant PLS-R predictors.

BRT	PLS-R
No. different disturbance types *	No. of patches *
Land use: forest *	No. different disturbance types *
No. of patches *	Form: punctiform *
Form: punctiform *	Duration: <1day (0.7%, 18th)
Frequency: steady diffuse	No. different land uses (1.7%, 16th)
No. different selectivities *	No. different selectivities *
Disturbance: macroherbivory	Land use: forest *
Season: 1st & 4th quarter *	Disturbance: single-tree-felling (1.1%, 14th)
Disturbance: foreign material	Season: 1st & 4th quarter *
Season: 1st to 4th quarter	Land use: grassland (1.8%, 15th)

To detect differences between forested and non forested plots further PLS-R analyses were conducted. It was expected that different disturbance regimes and lighting conditions affect species richness. Hence, for each patch as smallest land cover unit the size was calculated using GIS and the area of forested space was calculated for each plot. Species richness on plots with only little forest cover was mostly explained by heterogeneity (fuzzy variables) of the disturbance regime. Six variables explained 61% of diversity. However, the plots with highest forest cover showed a high prediction of 82% and a low error (4.7%) but needed eight variables for explanation, most of them from spatial categories of size, form and distribution. Both in common were the variety of land-uses within a plot. To enlarge the number of samples within a category, new subsets were calculated. The more open sets showed all the importance of number of different land-uses and patch number within the plots. Furthermore the sets 0-25% and 0-50% show the importance of forest as land-use, the sets 50-100 and 75-100% paths as land-use (Table 2-11).

Table 2-11: Subsets with 0-25%, 0-50%, 50-100%, and 75-100% forest within one plot, furthermore the subsets 0-5% and 96-100% as 'unforested' and 'fully forested' areas, respectively. Table shows PLS-R statistics and most significant positive and negative predictors.

Forest cover [%]	**N**	**R²**	**RMSE**	**Pred. error [%]**	**No. of signif. variables**	**No. of PLS-R axes**
0-5	61	0.61	18.1	5.9	6[a]	2
0-25	66	0.66	19.8	6.6	6[b]	4
0-50	73	0.76	20.3	6.4	8[c]	2
50-100	27	0.75	19.7	6.6	3[d]	2
75-100	20	0.87	15.5	5.2	4[e]	4
96-100	11	0.82	13.7	4.7	8[f]	5

[a] Model variables: correlated (no. patches; no. different selections; no. different disturbance types; no. different land uses; selectivity: age & species); anti-correlated (land use: grassland)

[b] Model variables: correlated (no. patches; no. different selectivities; no. different land uses; selectivity: age & species; land use: forest; disturbance: compaction (tracks)

[c] Model variables: correlated (land use: forest; no. patches; no. different selectivities; no. different land uses; disturbance: single tree felling; season: 1st & 4th quarter; form: punctiform); anti-correlated (land use: grassland)

[d] Model variables: correlated (land use: path; no. patches; no. different land uses)

[e] Model variables: correlated (land use: path; disturbance: foreign material; no. different distributions)

[f] Model variables: correlated (size: 4/4-area; land use: path; distribution: homogeneous; no. patches; no. different distributions; form: laminar; no. different land uses; no. different forms)

2.4.2.2 Beta diversity

After focusing on the α-diversity, a further focus was put on the β-diversity. Results show for Grafenwöhr Training Area an overall high to very high similarity between the different plots (Figure 2-18, right). Only in the western part of the sampling area, a medium similarity differs from the majority of area. Similarity index ranges from 0.49 – 0.75 for Grafenwöhr data. In comparing the kriging result with the forest map on the left side, one may discover a conformance with forested and non-forested areas. The hot spots of species richness just show intermediate similarity, but most of the area supports the interchange of species.

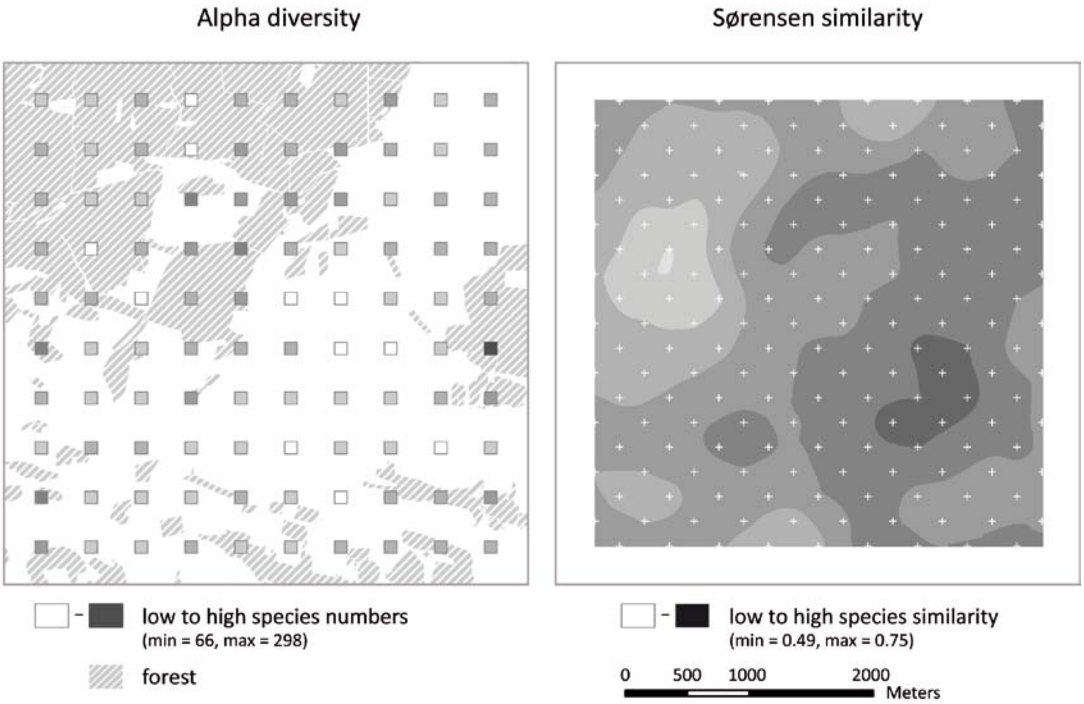


Figure 2-18: Alpha diversity and Sørensen similarity at Grafenwöhr Training Are. On the left side are the forested areas and the 100 plots with their species richness. The map on the right side (same scale) shows the values of the Sørensen-Similarity-Index, in-between-plot values are marked with small crosses. Kriging was used to derive these data, a technique to interpolate values at an unobserved location from observations of a known and nearby location. Colors are chosen from white (low species numbers; low similarity) to black (high species numbers; high similarity).

2.4.3 Land use and disturbances on patch scale

The analyses on landscape-level showed a high influence of the number of patches on plant species richness within one plot. These patches arise not only from the land-use classes on landscape level, but also from different disturbances and their scales. Thus, the complexity of the interactions on landscape scale needs a differentiated approach. Therefore, I focused on the patch scale to break analyses down to the influence of disturbances and their intensity and occurrence. Plant species numbers varied from 20 to 178 on the assigned patches, with a mean number of 66.9. Highest species numbers were found in forested patches, followed by fallow land and grassland.

2.4.3.1 Influence of land use, disturbances and disturbance descriptors on species richness

A PLS-R was conducted, using species richness as independent variable. A first analysis with the full data set reduced the number of variables to 12 significant ones, eliminating variables with weak explanatory force via jack knife procedure and by a manual elimination of variables with redundant information (Table 2-12).

Model quality was low ($R^2 = 0.2$). The model was stable with the reduced variables and showed an explanation of 20% on the first axis. The following axes did not bring further achievement. With a mean species richness of 66.9 on all patches root mean squares error was high (RMSE = 22).

Table 2-12: Summary of results of PLS-R of full Grafenwöhr data on patch level. Twelve significant parameters explained 20%.

N	R^2	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
595	0.2	22	12.4	12[a]	2

aModel variables: correlated (no. different selectivities; form: punctiform; land use: forest; no. different seasons; disturbance: wild boar; duration: <1day; disturbance: mowing); anti-correlated (land use: path; land use: water body; frequency: steady intense; form: laminar; season: 3rd & 4th quarter)

Particularly one group is striking which consists of the predictors with highest positive correlation: The land-use 'forest' with 'punctiform' disturbance, the 'number of different selectivities', and 'number of different seasonalities'. The first three mentioned are in somehow related to each other since selectivities are strongly related to forestry (age, species, location) and disturbances often punctiform, e.g., single tree felling.

2.4.3.2 Influence of forested and non-forested patches on species richness

In the analyses on plot scale the influence of forest clearly stood out. The mixed dataset including forested and open landscape patches did not give a sufficient explanation for species richness on local scale.

2.4.3.3 Analysis of open landscape patches

The 595 patches were separated according to their land-use category 'forest', resulting in 517 open landscape patches which were analyzed separately. Analyses show a poor explanation of only 13% with 11 significant variables that indicate some heterogeneity, punctual disturbance and the influence of fallow land (Table 2-13).

Table 2-13: Summary of results of PLS-R of open landscape patches at GW on patch level. Eleven significant parameters explained 13%.

N	R^2	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
517	0.13	22.4	14.6	11[a]	2

[a] Model variables: correlated (form_punctiform; no. diff.form; no.diff.sel; no. diff.seas; lu_fallowland; dur_<1day; dist_single_treefelling); anti-correlated (lu_path; lu_waterbody; freq_steadyintense; dist_foreign_material)

2.4.3.4 Analysis of forested patches

The 78 forested patches were analyzed separately and also showed a poor prediction of only 13% with seven parameters. Positive correlation showed the forest related variables heterogeneity of selectivity and age & species as combined selectivity. Negative correlation was related to the distribution of disturbances (Table 2-14). All three analyses on local scale, with full and splitted data set, showed poor explanation for species richness.

Table 2-14: Summary of results of PLS-R of forested patches at GW on patch level. Seven significant parameters explained 13%.

N	R²	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
78	0.13	31	17.4	7[a]	3

[a] Model variables: correlated (no.diff.disttypes; dist_compaction_wheels; no. diff.sel; sel_age_spec; no. diff.freq); anti-correlated (no.diff.distr; distr_homog)

2.4.4 Analyses including Ellenberg indicator values

A different approach is the application of Ellenberg indicator values (Schaffers & Sýkora 2000; Aavik *et al.* 2008). They estimate the optimal position of a plant species along an environmental gradient (Ellenberg 1991; Diekmann 2003). In the following sub-chapters these three analyses will be repeated, including the indicator values.

2.4.4.1 PLS-R with full data and Ellenberg indicator values

The first analysis was again with the full data set, extended by the Ellenberg indicator values as maximum, minimum and mean value for each patch. A comparison of the analyses with (a) and without (b) indicator values is displayed in table Table 2-15.

Adding Ellenberg indicator values increased explanation of species richness to 63% and reduced prediction error in the same time. The number of significant variables rose to 18 (mostly abiotic variables) and showed a high influence of the maximum values humidity, light, pH and nitrogen on the first axis, but also of forests and macroherbivory. Mowing and median and minimum pH values appear on the second axis (6%).

Table 2-15: Summary of results of LS-R of full Grafenwöhr data on patch level; a) corresponds to Table 2-12, b) includes Ellenberg indicator values.

	N	R²	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
a)	595	0.2	22	12.4	12[a]	2
b)	595	0.63	15	8.4	18[b]	4

[a] Model variables: correlated (no.diff.sel; form_punctual; lu_forest; no.diff.seas; dist_wildboar; dur_<1day; dist_mowing); anti-correlated (lu_path; lu_waterbody; freq_steadyintense; form_laminar; seas_3&4q)

[b] Model variables: correlated (F.max; L.max; R.max; N.max; dist_mowing; S.max; R.med; dist_macroherbivory; lu_forest; K.max; T.max); anti-correlated (L.min; T.min; F.min; R.min; K.min; N.min; form_laminar)

2.4.4.2 Analysis of open landscape patches and Ellenberg indicator values

Like in the chapter above, the dataset was splitted to figure out the influence of open or forested landscape variables to species richness. In open landscape the addition of Ellenberg indicator values shifted the prediction with nearly 50% to 62%. Here as well the error of prediction dropped but the number of variables increased. Results are displayed in Table 2-16.

Table 2-16: Summary of results of PLS-R of open landscape patches at GW on patch level; a) corresponds to Table 2-13, b) includes Ellenberg indicator values.

	N	R²	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
a)	517	0.13	22.4	14.6	11[a]	2
b)	517	0.62	13.5	8.8	16[b]	2

[a]Model variables: correlated (form_punctual; no.diff.form; no. diff.sel; no. diff.seas; lu_fallowland; dur_<1day; dist_single_treefelling); anti-correlated (lu_path; lu_waterbody; freq_steadyintense; dist_foreign_material)

[b]Model variables: correlated (N.max; dist_mowing; F.max; R.max; K.max; form_punctual; S.max; R.med; L.max; T.max); anti-correlated (L.min; T.min; F.min; R.min; N.min; K.med)

The first axis explained 60% of species richness. Maximum values of nitrogen and salinity, mowing and punctual form of disturbance showed a high influence and a cluster, like the maximum values of light, humidity, pH and continentality. The second axis added only 4% of explanation, with mowing, and N.min and R.med. The analysis showed a good linear prediction up to 130 plant species (max. 153).

2.4.4.3 Analysis of forested patches and Ellenberg indicator values

A last analysis with only forested patches showed a similar picture like in the open landscape (Tab). The explanation quintuples to 64%, with a reduced RMSE (11.2%) and a higher predictor number. The maximum indicator values of light, humidity, and pH, as well as macroherbivory and compaction by wheeled vehicles showed highest explanation on the first axis (63%). On second axis (6%) macroherbivory and a frequency of more than 3 times per year played the major role. Still, species numbers above 140 cannot be properly predicted anymore.

Table 2-17: Summary of results of PLS-R of forested patches at GW on patch level; a) corresponds to Table 2.7 1, b) includes Ellenberg indicator values.

N	R²	RMSE	Pred. error [%]	No. of significant variables	No. of PLS-R axes
78	0.13	31	17.4	7[a]	3
78	0.64	20	11.2	11[b]	3

[a]Model variables: correlated (no.diff.disttypes; dist_compaction_wheels; no. diff.sel; sel_age_spec; no. diff.freq); anti-correlated (no.diff.distr; distr_homog)

[b]Model variables: correlated (F.max; L.max; dist_compaction_wheels; R.max; dist_macroherbivory; R.med; freq_>3x/year); anti-correlated (F.med; L.min; R.min; K.min)

Including Ellenberg indicator values enhanced the explanation for species richness and indicates the importance of abiotic variables. Comparing the PLS-R results between open landscape and forest showed, that forest depend more on light and humidity, open landscape on nitrogen (Table 2-18 a-d).

Table 2-18: Comparison between forests and open landscape. A) Ellenberg indicator value 'light' (L); b) Ellenberg indicator value 'humidity' (F), Ellenberg indicator value 'pH' (R), Ellenberg indicator value 'nitrogen' (N). Displayed are the number of samples, the variance (min-max), median and mean value, standard deviation, and mean +/- standard deviation.

a) Light	Forest	Open landscape
No. of samples	5930	29893
Min - Max	1-9	1-9
Median	7	7
Mean	6.3	6.9
Std. dev.	1.45	1.03
Mean + std. dev.	7.75	7.93
Mean - std. dev.	4.85	5.87

b) Humidity	Forest	Open landscape
No. of samples	4922	25344
Min - Max	2-12	2-11
Median	5	5
Mean	5.8	5.2
Std. dev.	1.49	1.36
Mean + std. dev.	7.29	6.56
Mean - std. dev.	4.31	3.84

c) pH	Forest	Open landscape
No. of samples	3572	16833
Min - Max	1-9	1-9
Median	6	7
Mean	5.6	6.6
Std. dev.	1.77	1.35
Mean + std. dev.	7.37	7.95
Mean - std. dev.	3.83	5.25

d) Nitrogen	Forest	Open landscape
No. of samples	4984	25236
Min - Max	1-9	1-9
Median	5	5
Mean	5.1	5.1
Std. dev.	1.91	1.76
Mean + std. dev.	7.01	6.86
Mean - std. dev.	3.19	3.34

While the median is mostly identical, forests show a higher mean level of humidity than open landscapes (5.8 versus 5.2), and lower mean level of light (6.3 vs. 6.9) and pH (5.6 vs. 6.6). Nitrogen values are very similar. However, standard deviations show a broader range in the forested than open landscape and exhibit significant differences especially at the bottom end of the scale for pH (forest: 3.83; open landscape: 5.25) and light (forest: 4.85; open landscape: 5.87). Furthermore, forests show a higher species richness (Figure 2-19).

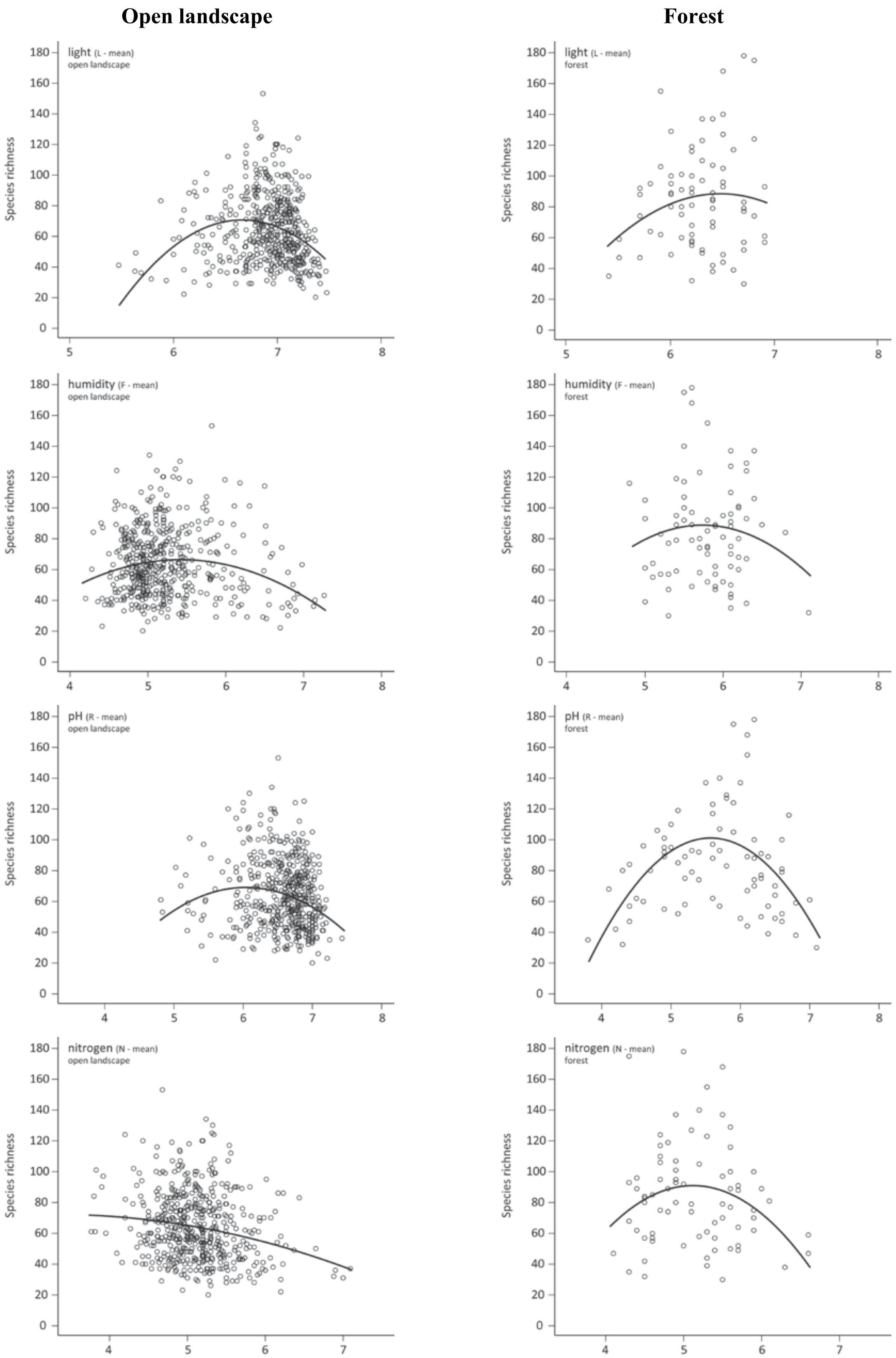


Figure 2-19: Quadratic regressions of species richness on the mean Ellenberg values for light (L), humidity (F), pH (R) and nitrogen (N). (a) Total number of species vs. light (open landscape); (b) total number of species vs. light (forest); (c) total number of species vs. humidity (open landscape); (d) total number of species vs. humidity (forest); (e) Total number of species vs. pH (open landscape); (f) total number of species vs. pH (forest); (g) total number of species vs. nitrogen (open landscape); (h) total number of species vs. nitrogen (forest).

2.4.5 Threatened and endangered species

Numerous threatened and endangered species of the Bavarian Red List (RL) were recorded (Figure 2-20). Three fourths of the 595 patches showed at least one rare species (Figure 2-21), predominantly on the three principal land-use types (Fig 22). Fallow land hosted most of the endangered species (38.5%) (Figure 2-22, full list in supplement S 2). Besides the single occurring Red List-1 species *Lysimachia punctata*, these were every third species of category two and three, as well as 40% of species from the early warning list. Grassland hosted 21%, forests 15% and transition zones 11% of all recorded rare species, respectively (Figure 2-21).

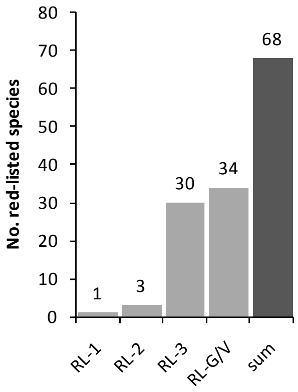


Figure 2-20: Number of red-listed species at Grafenwöhr. Categories are: critically endangered (RL-1), endangered (RL-2), vulnerable (RL-3), threatened /near threatened (RL-G/V). In sum, 68 threatened an endangered species were recorded.

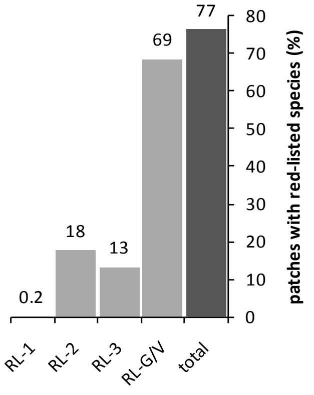


Figure 2-21: Occurrence of red-listed species categories on patches. Numbers display proportion of occurrence. 100% = 595 patches. A total of 77% of all patches presented at least one red-listed species.

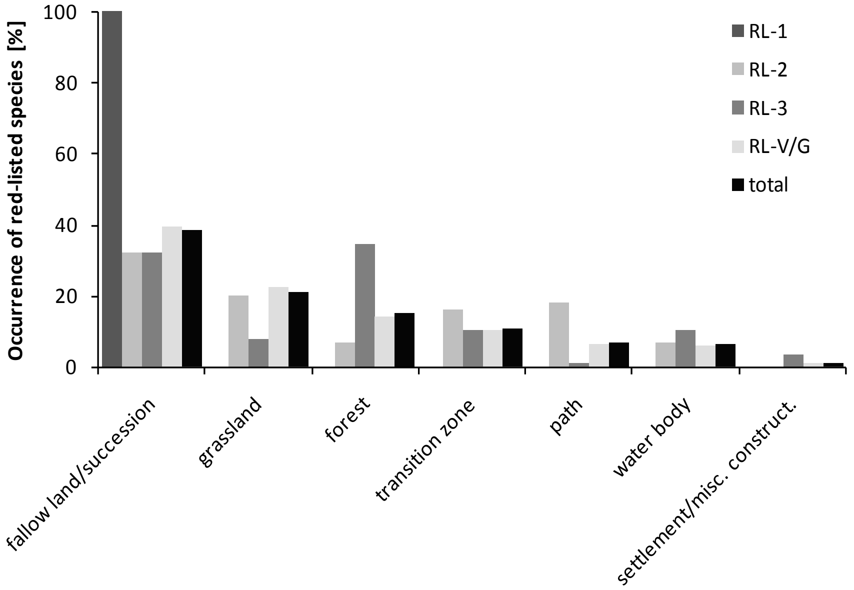


Figure 2-22: Land-use types and red-listed species. Displayed is the proportion of red-listed species on a certain land-use type. As example: All recorded RL-1 species was recorded on fallow land.

Most threatened and endangered species were found in areas which were disturbed by wheeled vehicles (22.6%), macroherbivory (15.2%), tracked vehicle (13.9%) and mowing (9.7%). However, because of mostly overlapping disturbances, it is difficult to distinguish, if endangered species can be related to a single disturbance type. For example, the only individual of the Red List-1 species is related to compaction by wheeled vehicles, clear felling, macroherbivory and compaction by trampling (full list in supplement S3).

The most common rare species were the near threatened (RL-V) species *Silaum silaus* (190 of 595 patches), *Rhinanthus minor* (183 patches) and *Dianthus deltoides* (93 patches). The endangered (RL-2) species *Lathyrus nissolia* found ideal conditions on 92 patches.

Threatened and endangered species at Grafenwöhr Training Area will be considered more detailed in chapter 4.

2.4.6 Influence of military training on grassland diversity

As previously mentioned, one third of the study area was classified as grassland. These areas are widely used for training activities using tanks. The use of tanks results in linear compacted soil, destruction of the vegetation cover, soil exposure, and the creation of small sized depressions (Figure 2-23). In order to set up a similar base for the analysis of the influence of military maneuvers on grassland diversity, areas for survey were chosen that are characterized by an annual mowing regime.

Figure 2-23: Tracks and destruction in grassland after tank driving. Pictures show a water filled depression after excavation or tank turn (left) and tank tracks on moderately mowed meadows (corridor strips).

In order to identify other factors influencing species richness, plots were separated into two different types: single-patch grassland plots (1-ha size), which allow for the focus on the military actions, and multi-patch grassland plots, which may be affected by neighbouring patches.

Five single-patch grassland plots were found in the dataset, four of which were influenced by the use of tanks (considered here as disturbed), and one of which was without tracks (considered here are undisturbed) (Figure 2-24a).

A total number of 156 plant species were recorded within the single-patch plots. Comparing disturbed and undisturbed plots, a substantial difference in species richness is evident. Track covered plots exhibit a total number of 126 plant species, whereas the undisturbed plot contains approximately half the number of species. The disturbed and undisturbed single-patch plots had 38 species in common. The undisturbed plot contained 28 unique plants. The 88 unique species of the disturbed plots included water plants (18) and crop plants (11).

In comparison, these analyses were again conducted on multi-patch plots, following the question, if tank training activities superimpose other possible effects from the surrounding areas. For this, 36 disturbed and 27 undisturbed patches were surveyed (Figure 2-24b). Multi-patch plots contained a total number of 326 plant species, more than twice the number of single-patch plots. However, the difference between multi-patch plots with and without military disturbance was indistinct.

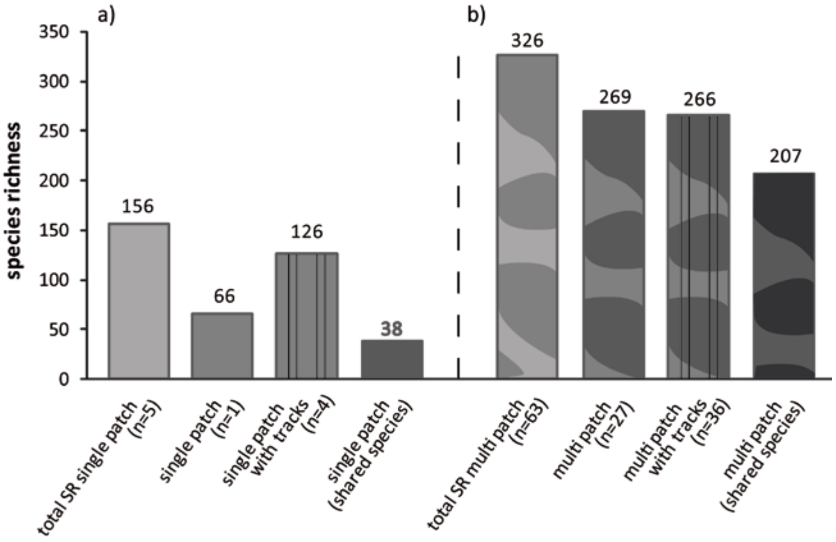


Figure 2-24: Comparison of species richness within a) one-patch and b) multi-patch grassland plots and the influence of military tank training (with tracks) on species numbers.

2.5 DISCUSSION

It was expected that Grafenwöhr Training Area is a great example for a heterogeneous landscape. Within the seven land-use types, traces of thirty-five different disturbance types were found. Several disturbances were ubiquitous, especially the compaction by wheeled vehicles, disturbances by tracked vehicles and tracks and biting marks of deer and wild boar (macroherbivory). These disturbances can be related to the main objective of the study site, the military training, but also to the naturalness of the site with its nearly undisturbed wildlife. Several important disturbances were related to the maintenance of the area. These are mainly the road works (gravel roads, banks) and the extensive mowing, but also the controlled burning of vegetation. The mixture of disturbances within the same area with the intentions of either military training or maintenance work and the influence of undisturbed natural dynamics, create a small scaled landscape mosaic with very different temporal and spatial characteristics. Therefore, the hypothesis was confirmed.

It was further assumed that the heterogeneity of the landscape influences species richness. With simple linear regressions I could prove this hypothesis. The more land-use types, disturbance types and different patches within a hectare-sized area, the more species were found. This is supported by several studies (e.g., Báldi 2008; O'Dwyer & Green 2010). However, the highest species numbers were not related to the highest number of different disturbances or land uses. One aspect is that temporal and spatial interactions play an important role apart from the heterogeneous plots (multipatch concept, Jentsch 2007). The different intensities and dynamics of disturbances lead to a broad range of environmental processes, like succession and resilience after disturbance (Milchunas *et al*. 2000; Díaz *et al.* 2005). These dimensions cannot be displayed in a simple regression. Patches were distinguished between their land use and their disturbance regime. Most patches showed overlapping disturbance types that were characterized by different temporal and spatial dimensions. Multivariate statistics enables to include all these parameters. The new analyses showed that only two third of species can be explained with the land-use and disturbance regime, despite this high amount of predictors.

Therefore I included abiotic factors as a second aspect, because they can essentially influence local biodiversity. According to Waldhardt *et al*. (2004), soil type would be one important parameter. Tsegaye & Hill (1998) stated that variability in soils may lead to a heterogeneous plant growth and would therefore support biodiversity. I decided to include Ellenberg indicator values. They characterize the habitats for most plant species. First, soil samples were not available due to security reasons (blind shells in the soil). Second, punctual soil samples do not represent a heterogeneous patch with a size of up to one hectare. The inclusion of Ellenberg indicator values has the advantage that the heterogeneity of a landscape and local abiotic conditions are displayed in these values.

In my analyses on patch scale, the indicator values tremendously increased the explanation power of previous analyses without abiotic information. The poor explanation of these first analyses nearly quintupled. But results show also that the disturbance regime plays an ostensible secondary role. Most important abiotic factors were humidity, light, pH, and nutrients. These abiotic factors interact under special conditions and consequently determine resource availability. A higher pH has a positive effect on nutrient availability for plants (e.g. as NO_3^-) and neutral to slightly basic soils show a higher activity of nitrifiers (Falkengren-Grerup *et al.* 1998; Härdtle *et al.* 2003). Yet, plants need soil humidity to uptake these nutrients (Metwally & Pollard 1959; Misra 2003). Humidity is altered by the influence of light. Furthermore, a higher light availability in forests permit grassland plant species to establish (Vockenhuber *et al.* 2011) and thus can enhance biodiversity in understory layers (Härdtle *et al.* 2003; Hofmeister *et al.* 2009). Whereas, the limitation of resources, in particular light, soil moisture and nutrients, reduce secondary metabolism and resistance against herbivores (Herms & Mattson 1992).

Besides heterogeneity indicators and abiotic parameters, my analyses also showed an influence of land use and disturbance types. Emanuelsson (2009b) stated that semi-open landscapes show greater plant diversity than either forests or pure open landscapes. With my data, I can partly support his conclusion, because most plant species were recorded on fallow land. However, unexpected high influence showed forests and several associated spatial and temporal parameters, which were considerably more than factors of the open landscape. But why are the forests of Grafenwöhr that species rich? I see two reasonable explanations. The first explanation, which is indicated by the number of species, is related to a certain disturbance type, are moderate forest operations, like conservative tree removal (grove felling, single tree felling) and resulting skidding tracks. A second explanation could be the mostly semi-natural state. Forests at Grafenwöhr show a mix of deciduous trees and conifers. They are sparser than forests, which are subject to silviculture. A sustainable maintenance of the forestry department keeps several wooden areas abandoned. In consequence, to give one example, wind fall does not only open gaps in the canopy, but also deadwood is left on the ground, giving habitat for numerous species.

Yet, it is not possible to separate land use or disturbance from abiotic parameters, since there is a reciprocal relationship (Ettema & Wardle 2002). An open tree cover can alter abiotic factors, whereas the soil conditions determine the aboveground vegetation (Quilchano *et al.* 2008). In European deciduous forests most plant species occur in the herb layer (Gilliam 2007). Several studies prove that diversity in this layer depends on soil pH, nutrient and light availability (Härdtle *et al.* 2003; Hofmeister *et al.* 2009; Axmanová *et al.* 2012) and soil moisture (Qian *et al.* 1997). Other authors see no effect and deny the importance of light to species diversity (e.g., Lenière & Houle 2006). Since influence of light in forests strongly depends on the structure and cover of tree crowns, the effect is a matter of species (Jennings *et al.* 1999). Especially military training can alter the availability of resources (Garten *et al.* 2003; DeBusk *et al.* 2005; Liu *et al.* 2010). Some of the most severe damages happen due to tank driving training. Hirst *et al.* (2003) report a significant visibility one year after a tank was driving on grassland. Disturbances by tracked vehicles did not play a role in Grafenwöhr according to my PLS-R analyses. Still, patches with identified tank tracks had the third-highest species number. An analysis, assuming identical basic conditions concerning land-use type and regular disturbance regime (grassland and mowing), showed significant differences in species richness with tank driving as additional disturbance. Admittedly, the reference of missing tank disturbance consisted of only one plot. Thus, my results are not statistically valid. But can they be seen as indicator of the influence of tank driving? Prosser *et al.* (2000), for example, did not find any changes in plant species composition due to tank driving.

The multi-patch approach doubled the total species richness without additional military disturbance. Additional tank disturbance, however, did not additionally change species richness. Therefore, I conclude that tank maneuvers on grassland create new habitats, especially due to open soil and altered humidity, but these effects are exceeded by multiple disturbances and associated parameters, as much as abiotic conditions. However, species react in a different manner on disturbances. Orth & Warren (2006), for example, stated that only every eighth of their recorded threatened and endangered species found on military lands were clearly dependent on disturbances, whereas nearly every second species showed antagonistic effects. The percentage of disturbance-tolerant species could not exactly be determined.

Disturbances with a wide spectrum of intensity create small niches. Because of the continuous natural and anthropogenic disturbances, a variety of conditions are simultaneously present; active disturbance, recovery and natural succession are occurring at the same time. Therefore, one might expect a high dissimilarity between the plots, and consequently high beta diversity. Tough, kriging of the Sørensen similarity shows only intermediate similarity in forested plots and high similarity in the open landscape. But what explains the throughout high species richness at GTA and the apparently good possibility for dispersal and species interchange? A major reason is that, in contrast to an agricultural landscape, it is not designed with strictly defined areas and boundaries. Moreover, species are not subject to crop rotation and farming practices, with fertilizers and pesticides that alter richness and composition and function as filter for seed dispersal. Due to military training, there is traffic across the whole area. Maneuvers take place in the open and semi-open landscape. Thus, seeds can be distributed by tanks and trucks in tracks and wheels. The maintenance of the landscape, primarily mowing, is conducted in a very extensive way with some time lag between the zones and wide corridors for wildlife which serve as another disperser.

The lower similarity of forests can be related to different factors. Several sectors are restricted for any military use and forestry is set to a minimum, whereas other sectors are open for training.

Therefore dispersal might be reduced in some areas whereas in others, also grassland species are distributed because of the environmental conditions (e.g., light) and their dispersal.

Trame (1997) stated that "rare species exist to a remarkable extent on military installations, even in the presence of military training". We could change the second part into 'because of the presence of military training'. A species is threatened or endangered, when a land-use change either increases the impacts or leads to abandonment, in other words, when conditions of its habitat are altered (Lindborg & Eriksson 2004a). The word 'because' can be seen negatively or positively. On military training areas, disturbances partly are very high with severe destruction of vegetation cover and soil. Until the mid 1990s, military training caused massive soil erosion at Grafenwöhr. In starting erosion control measures (e.g., blocking areas, detention reservoirs, seeding), these impacts have been reduced (Rieck & Meier 2010). Thus, are the rare species remnants of this area of changing conditions? Or does the military training area function as refugia for threatened species from outside the area, which is supported by the military training? The answer might be both. Species numbers abundance certainly was reduced during the training. As stated by Marhoul & Zámečník (2012), not all species can tolerate disturbances. However, these reduced species very likely had failed to make it on the Red List, because this list includes vegetation samplings from a larger scale. Species, that are listed, are classified as rare in the state of Bavaria. Consequently, the training area is host to these species. This is partially apparent in my records, since several species that are listed, show a remarkably abundance in numerous patches. Presence and absence sampling do not reflect the cover and abundance of a single plant species within a patch, but across patches. One of these species is the endangered (RL-2) grass-vetchling (*Lathyrus nissolia*) which was found on every fifth open landscape patch. The plant is native to weed fields with nutrient-poor and dryer conditions. Since fields mostly are fertilized, conditions have negatively changed. The plant shows some disturbance tolerance, and therefore could establish and build up a stable population at Grafenwöhr (Griese 1989). Because disturbances enable early succession stages, less competitive species, like endangered plant species, are supported (White & Jentsch 2004; Jentsch 2007).

Chapter 3

3 LAND USE AND DISTURBANCE REGIME IN AGRICULTURAL LANDSCAPES: WHAT EXPLAINS SPECIES DIVERSITY IN COMPARISON WITH A SEMI-NATURAL LANDSCAPE?

3.1 INTRODUCTION

In a second approach, I focus on the disturbance regime of typical agricultural landscapes in central Europe and compare it with the semi-natural landscape of chapter two.

The two study areas, situated in the northern part of Bavaria, display the typical structures of a cultural landscape. These are forest, agricultural land, meadows, settlements and infrastructure. Agricultural land covers approximately 190,000 km² (52%) of Germany's total land area, forests cover 108,000 km² (30.2%) (Statistisches Bundesamt 2012).

Agriculture and forest management have been part of our landscapes for millennia (Svenning *et al.* 2009; Eriksson 2012). Within the last century, land-use intensification and the associated disturbance regime have led to major concerns about the effects on species diversity in agricultural landscapes (Mander *et al.* 1999; Luoto 2000). The environment faces three major problems with agricultural land use. The first problem is the homogenization of the landscape. What happens on fields is actually a synchronization of temporal and spatial parameters due to sowing and harvesting (Baessler & Klotz 2006; Belfrage *et al.* 2006; Warren *et al.* 2007; Geiger *et al.* 2010; Karp *et al.* 2012). This leads to an ecological simplification of the landscape (Zechmeister *et al.* 2003; Firbank *et al.* 2008; Liira *et al.* 2008).

The second problem is the fertilization and application of herbicides and insecticides. Nature of crop cultivation is to achieve a maximum of quantity and purity in a monoculture for economical reasons (Albrecht *et al.* 2009). Therefore, the system requires to push the wanted species. Other plants, although they would enhance diversity, are handled as weeds and need to be controlled (Moser *et al.* 2002; Marshall *et al.* 2003). Most of the available fertilizers and pesticides directly affect flora and fauna (Clark & Tilman 2008). Additionally, special crops are sown at high densities, which lead to a high competition for light and disadvantage even for established but low-growing species (Bischoff & Mahn 2000). Several studies show that adding nitrogen reduces species richness (e.g., Stevens *et al.* 2004; Roth *et al.* 2013). Wilson & Tilman (2002) report that in combination with increasing disturbance, nitrogen application leads to a replacement of annual plant species to perennials.

The third problem is the impact of heavy vehicles. The use of heavy machinery has changed soil characteristics (Geiger *et al.* 2010). Usually we find a linear shaped compaction of the soil, which alters the physical characteristics, like pore size, bulk density and water permeability (e.g., Doneen *et al.* 1952; Lull 1959; Vollmer *et al.* 1976; Arvidsson *et al.* 2011), which influences soil water content, root penetration and more.

Moser *et al.* (2002) and Belfrage *et al.* (2006) found out that not only human influence but also size and shape of fields influence biodiversity. For example, Belfrage *et al.* (2006) detected a bisection of bird species on larger farms than on smaller ones. This confirms the theory that larger areas have a higher potential for increased species richness due to more potential niches (Rosenzweig 1995; Crawley & Harral 2001). However, their study has been conducted on an organic farm. In intensively used agricultural landscapes one has to put the heterogeneity of a landscape into question. Semi-natural habitats like field boundaries and hedge rows have been drastically reduced (Robinson & Sutherland 2002; Luoto *et al.* 2003). Abiotic factors, like pH or nutrient supply, lose importance due to this homogenization and regulation and change abruptly (Beierkuhnlein 2002). Succession and dispersal are reduced or even impeded. Noteworthy is that this happens independently from the size of the fields. One homogenized field of 100 hectare size does not differ from 10 fields with a size of 10 hectares (Kleijn *et al.* 2009), if treated the same way.

However, it is often neglected that in agricultural landscapes a large number of habitats and niches exist that cannot be found in natural landscapes (Luoto 2000; Benton *et al.* 2003; Zechmeister *et al.* 2003; Billeter *et al.* 2008). Especially smaller fields might show a higher variety within the same section of landscape because of the handling of different farmers and the cultivation of a variety of crops (Fahrig *et al.* 2011). In between these fields we may find transitions zones and boundaries that usually abruptly separate patches (Wiens *et al.* 1985; Forman 1995b; Ma *et al.* 2002; Zechmeister *et al.* 2003).

These semi-natural habitats or ecotones (Livingston 1903; Clements 1905) give space for anthropogenic and natural disturbances, facilitate succession in different stages and enhance species diversity (Duelli 1997; Aavik *et al.* 2008), not only in the certain habitat (alpha diversity) but also on landscape scale (gamma diversity - Whittaker 1960, 1972). These different stages of succession in time and space furthermore offer room for disturbances in an intermediate level, which, according to Grime (1973) and Connell (1978), maximizes species richness. Still, there is a relevant external influence on boundaries. Ma *et al.* (2002) described a gradient of physical, chemical and biotic conditions in buffer zones, influences by adjacent fields. Smart *et al.* (2002) surveyed grasslands with different productivities. At lower productivity, the boundaries had less species than the grassland itself. With increasing intensity, however, the number of species reduced at a faster rate within the meadow than in the adjacent transition zone.

Figure 3-1: Landscape transition from small (left) to large scale agriculture (right). Painted by G. Brusewitz, Sweden. Source: Belfrage *et al.* 2006)

Most forests in Europe have been planted and cover formerly deforested areas (Gilliam 2007). Since wood has always been an important resource, often fast growing kinds of wood has been planted (e.g. spruce). Forests are often highly fragmented in agricultural landscapes (Dumortier *et al.* 2002). One reason for a reduction in species richness is the short distance to human settlements (Gilliam 2007). They are used for industrial products and energy generation (Mantau 2012). Anthropogenic disturbances in forests contain several cutting techniques (e.g., clear cutting, single tree cutting, grove felling). After clear cutting, tree nurseries become established which cause some ecological impact (Shear & Stewart 1934). In former times this used to happen on larger scales, leading to a homogenization of species and stand age (Pitkänen 2000). Furthermore, highly maintained forest grounds are cleaned of dead wood and show linear features like the scars of skidding tracks and compacted soil (Greacen & Sands 1980; Frey *et al.* 2009).

On the contrary, natural forests are heterogeneous mosaics of different ages and successional stages (Spies & Turner 1999). Highest diversity is found in the herbaceous layer of forests (Gilliam & Roberts 2003; Gilliam 2007). Plant species on the forest floor are depended on the trees (Quilchano *et al.* 2008). They regulate the light availability and quality of radiation on the ground (Canham *et al.* 1994). Furthermore amount and quality of litter lead to differences of nutrient availability and mineralization (Gallardo & Merino 1993; Saetre & Bååth 2000), but also soil pH (Scheffer *et al.* 2002). Water availability in forests is depended on the permeability of the tree cover for precipitation, but also on evapotranspiration and microclimate (Zon 1945; Kupfer *et al.* 2006). Obviously, we find big differences between deciduous forests and coniferous forests which are related to their cover density, to the season and to litter decomposition. In general, forests are not subject to fertilization. Sometimes liming is conducted to countervail soil acidification (Scheffer *et al.* 2002). Apart from large scaled clear cuts or tree nurseries as monocultures, homogenization of forests is kept within a limit.

The characteristics and structural differences in cultural landscapes lead to the question, what are the significant drivers for species richness. We expect clear differences between the influences of agricultural and semi-natural landscapes in case of species diversity. Besides abiotic factors, the heterogeneity of the system and the different disturbance regimes are expected to play a major role.

HYPOTHESES

- H1) Bedrock is a superior driver of species richness. I expect a higher species richness on calcareous than on siliceous ground.
- H2) Land use (agricultural, semi-natural) is the second most important driver.
- H3) In the semi-natural landscape, the overlapping anthropogenic and natural disturbances lead to a high heterogeneity as compared to the agricultural landscapes.
- H4) The type of disturbance is less important than the combination of various disturbances at plot (landscape) and patch (local) scale.
- H5) The disturbance regime is more important than abiotic heterogeneity and patch size in agricultural landscapes due to the homogenizing effect of agriculture at patch scale.
- H6) The common hypotheses HDH and IDH are valid.

3.2 STUDY SITES

The agricultural landscapes of Fichtelgebirge and Frankenalb are located in Upper Franconia, Bavaria, and approximately 60 km apart.

(1) Fichtelgebirge

The study area of Fichtelgebirge is located between the villages of Kirchenlamitz and Weissenstadt (32U 709 860E, 5557570N). Bedrock is of granite and phyllite (Retzer 1999). Soils consist of cambisols and podsols. The altitudinal gradient is between 650 and 800 m a.s.l., whereas the highest elevation of the Fichtelgebirge reaches 1053 m a.s.l. Mean precipitation is 1100 mm, mean annual temperature is 6 °C (Retzer 1999; Jentsch *et al.* 2012). The study area is south-east exposed and exhibits a short growing season of four months (Buhk *et al.* 2007b).

The landscape is characterized by an intensive agricultural land use for forest products and hay and silage. Furthermore, there are small settlements scattered within the area.

(2) Frankenalb

The study area of Frankenalb is located south of Pottenstein (32U 671190E, 55129710N). Bedrock is of Jurassic limestone. Soils consist of cambisols and luvisols on the plateaus and rendzina and terra rossa in the areas with slowed soil development (Retzer 1999). Within the study area we find an altitudinal gradient from 450 to 580 m a.s.l. which is north-east exposed. Annual precipitation varies between 600 and 900 mm (Heubes *et al.* 2011). Mean annual temperature is 7-8 °C. Therefore the survey area is in the transition area between oceanic and continental climate (Müller-Hohenstein 1971).

The northern Frankenalb has been used for agriculture since the Neolithic period, but under natural circumstances we would find predominantly beech forests (Neßhöver 1999). Nowadays the area is characterized by a small scale mosaic landscape with high land use diversity, consisting of forests, fields, meadows and pastures (Neßhöver 1999; Jentsch *et al.* 2012).

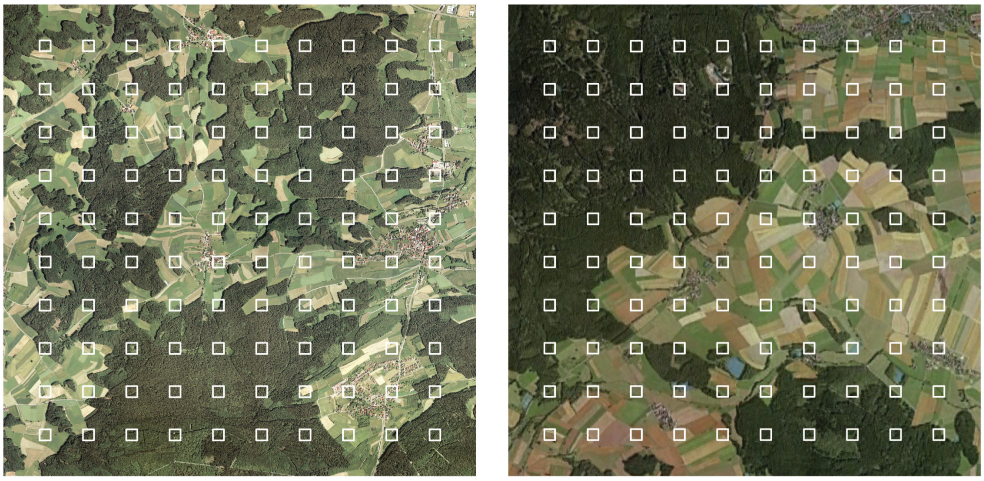
(3) Grafenwöhr Training Area

Grafenwöhr Training Area is located between the name giving town of Grafenwöhr to the east, Auerbach in der Oberpfalz to the west and Vilseck to the south in the administrative district of Upper Palatinate (Oberpfalz) about 90 km northeast of Nürnberg (32U 69400E, 5508300N). The eastern part of the area is characterized by Triassic sandstone and sandy soils, whereas the western part of the area, where the survey plots were placed, mostly Late Jurassic sediments of lime and dolomite are found, covered by dry Cretaceous sands. Keuper and Lias may be found in areas where ridges cut through the relief. At some locations, such as Rattenleite, spring horizons resulting from ground-water retaining clay horizons can be found. Mean annual precipitation is approximately 740 mm, and mean annual temperature is 7.3 °C (Climate Stations Grafenwöhr and Eschenbach, German Weather Service).

The area has been used for military training since 1907 and was repeatedly enlarged (Burckhardt 1994) to 23,000 ha of size. Besides the military training, maintenance is conducted in the form of road works and extensive mowing and forestry. The area is closed to the public.

The Leibniz Institute of Ecological Urban and Regional Development created a classification of human influence on the environment, the so called 'hemeroby index' (www.ioer-monitor.de). The closeness to nature is calculated and displayed in categories, reaching from 1 (ahemerobic, e.g. bare rocks, potential natural vegetation cover) to 7 (metahemerobic, e.g. fully sealed areas like industrial sites) (Walz & Stein 2014). The three study sites are located between the categories 3 (mesohemerobic - moderate human impact) and 4 (β-euhemerobic – moderate to strong human impact). The index is available from federal to municipality scale. In detail, Grafenwöhr was assigned to an index of 3.58 (map of Neustadt/Waldnaab). The community of Gößweinstein in the western part of the Frankenalb study site reached an index of 3.66 (map of Forchheim), Pottenstein in the eastern part 3.84 (map of Bayreuth/Land). Fichtelgebirge study site reached 3.88 in Kirchenlamitz and 3.9 in Weißenstadt (map of Wunsiedel i. Fichtelgebirge).

Frankenalb (FA) Fichtelgebirge (FG)



Grafenwöhr Training Area (GW)

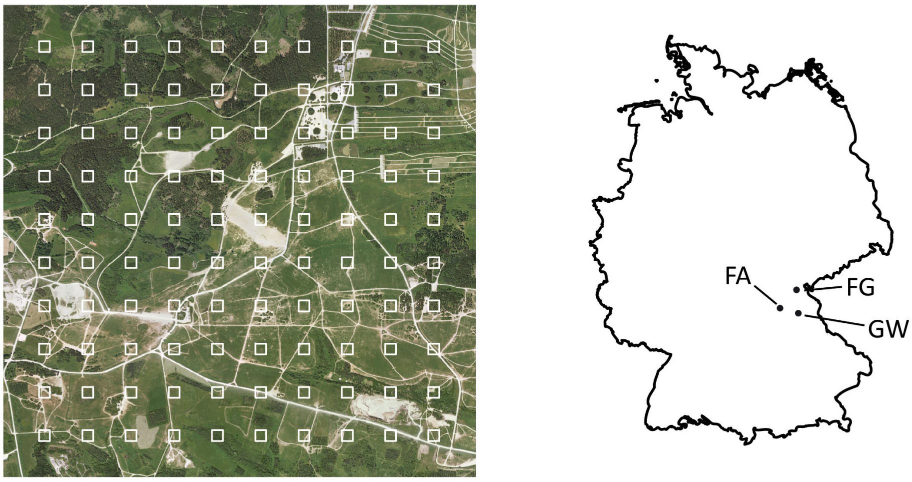


Figure 3-2: The three study sites: Frankenalb (32U 671190E, 55129710N), Fichtelgebirge (32U 709860E, 5557570N) and Grafenwöhr Training Area (32U 69400E, 5508300N). They are located within 60km distance in northern Bavaria, Germany.

3.2.1 Land-use types at Fichtelgebirge and Frankenalb

Both data sets exhibit the three main landscape types which are typical for agricultural land, i.e. forests, crop land and grassland. The three dominant land cover types sum up to 85% to 90% of each survey area. Smaller areas are covered by water bodies and transition zones between habitats. Both survey areas are crossed by numerous smaller roads that connect small villages (settlements) situated within the areas (Figure 3-3).

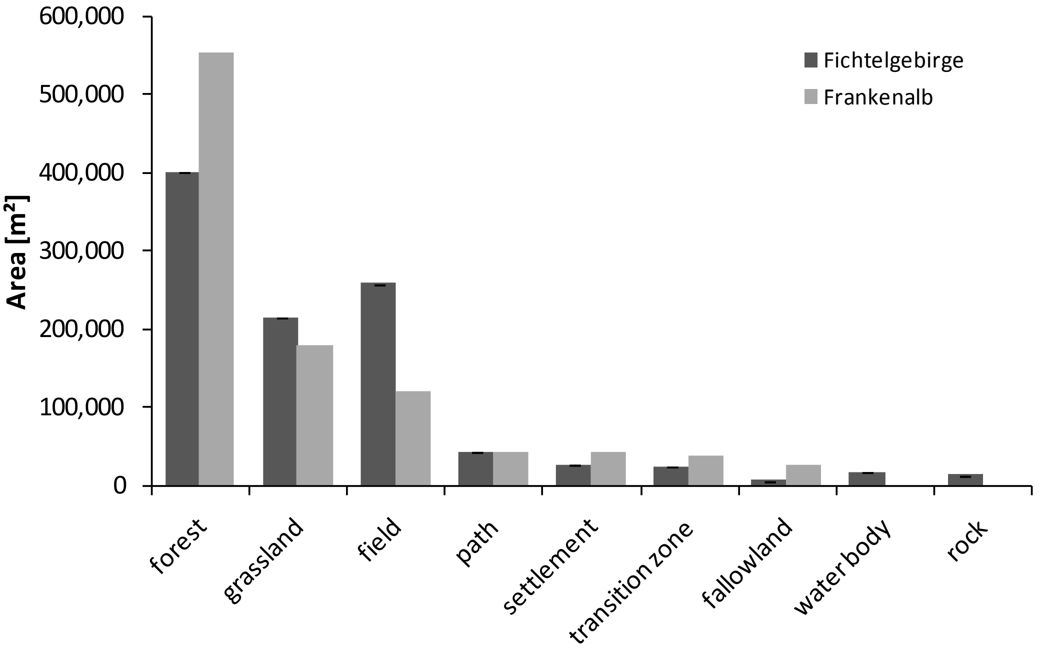


Figure 3-3: Total area covered by the different land cover types at Frankenalb and Fichtelgebirge.

Biggest differences between Fichtelgebirge and Frankenalb are the proportion of forest and fields. In Fichtelgebirge, 40% are covered by forests, whereas at Frankenalb, these are 55%. Fields for crop cultivation sum to 26% at Fichtelgebirge and to 12% at Frankenalb (Table 3-1).

Table 3-1: Proportion of land cover types at Fichtelgebirge and Frankenalb. Forests, grassland and agricultural fields cover approximately 90% on both study sites.

Land use type	**Fichtelgebirge (%)**	**Frankenalb (%)**
Forest	40.1	55.2
Grassland	21.5	18.0
Fields	25.8	12.0
Path	4.3	4.3
Settlement	2.6	4.2
Transition zone	2.5	3.7
Fallow land	0.6	2.6
Water body	1.7	0.0
Rock	1.3	0.0

Although more than half of the survey area of Frankenalb is covered by forest the mean size is just approximately 2,000 m² (3,700 m² at Fichtelgebirge). Special features are the rock formations at Fichtelgebirge with a maximum covering area of 6,000 m².

3.2.2 Disturbance types at Fichtelgebirge and Frankenalb

At Fichtelgebirge, 21 different disturbance types were recorded, at Frankenalb 25. Seventeen of them were found in both survey areas. Both data sets showed a high occurrence on compaction by wheeled vehicles. At Fichtelgebirge, nearly 40% of all patches were subject to mowing and 20% to agricultural land use. The high number of disturbances related to forestry, i.e. grove felling and thinning, correlated with the higher proportion of forests at Frankenalb. At Fichtelgebirge, the application of pesticides has not been recorded. However, it can be considered a certainty that in an agricultural landscape with nearly 26% of field cover agrochemicals were applied. The high number of patches with pesticides application (289) compared to the smaller number of agricultural land use (66) was the result of agrochemicals also applied on grassland and transition zones (Table 3-2).

Table 3-2: Disturbance types and their occurrence on patch-level at Frankenalb (FA) and Fichtelgebirge (FG).X indicated parameter: information about pesticides were not sampled but application was confirmed.

FG patches	Disturbance type	FA patches
100	Agriculture/ploughing	66
1	Biomass-input	43
28	Breakage	29
8	Clear felling	44
36	Compaction (trampling)	0
197	Compaction (wheels)	209
0	Creek allocation	1
0	Deadwood collection	4
6	Dehydration	1
5	Farming	8
0	Fencing	2
10	Flooding	0
1	Foreign material	0
0	Gardening	12
14	Grove felling	187
0	Macroherbivory	26
0	Material storing	1
3	Microherbivory	1
205	Mowing	38
1	None	1
x	Pesticides	289
4	Pond drainage	0
1	Quarry	36
24	Rejuvenation	38
95	Single tree felling	52
27	Skidding track	36
0	Soil/rock movements	2
9	Thinning	145
4	Wood storage /movement	30

3.2.3 Sampling methods

In this chapter, three data sets will be used for the analyses. Besides the two data sets of Fichtelgebirge and Frankenalb, the data of Grafenwöhr Training Area, as described in chapter two, were included. The surveys were conducted in different years and by different field teams.

1) Fichtelgebirge: Sampling was conducted in 2005. Responsible scientists were Constanze Buhk (née Ohl) and Anke Jentsch, vegetation experts were Thomas Blachnik and Andreas Barthel.

2) Frankenalb: Sampling was conducted in 2006. Responsible scientists were Vroni Retzer and Anke Jentsch, vegetation expert was Andreas Barthel.

3) Grafenwöhr: Sampling was conducted in 2008. Responsible scientists were Martin Alt and Anke Jentsch, vegetation expert was Alexander Ulmer.

Identification and labeling of plant species was done after the nomenclature of Jäger *et al.* (2005) and Möhl & Eggenberg (2007).

Sampling was conducted using a regular grid with a quadratic shape and evenly distributed plots of one hectare size. However, the first sampling in the Fichtelgebirge in 2005 was conducted on not 100 but 109 plots (results see Buhk *et al.* 2007b). Since Frankenalb and Grafenwöhr were sampled on 100 plots only, the additional Fichtelgebirge plots were left out in my analyses. The grid was placed in the landscape using aerial images in ArcGIS (ESRI Inc. 1999-2008). By means of topographical maps and aerial images, land-use classes and disturbance types were recorded in the field, as well as temporal and spatial parameters and information about the selectivity of a disturbance. For each allocated patch higher plant species were recorded. Sampling methods are explained in detail in chapter 2.2.1.

3.3 STATISTICAL METHODS

Methods are mainly described in chapter 2.3. Parameters for statistical analyses were identical with the ones used at Grafenwöhr. This was possible because all land-use parameters, disturbance types and temporal and spatial information were included into the analyses, even if they were unrepresented. Parameters were included binary coded (i.e. presence/absence) and therefore got automatically excluded with zero values only.

For analyses with all three data sets, further variables that indicate survey area were included. These were ‘Fichtelgebirge’, ‘Grafenwöhr’ and ‘Frankenalb’ for presence/absence information. A further category was ‘data base’ as categorical variable (GW = Grafenwöhr; FG = Fichtelgebirge; FA = Frankenalb) (Table 3-3). These categorical variables were used for displaying results.

Table 3-3: Table of parameters for multivariate statistics on plot (landscape) level.

Category	**Variables**
General information:	species richness/patch; size [m²]; data base (GW, FG, FA); Grafenwöhr (1/0); Frankenalb (1/0); Fichtelgebirge (1/0);
Fuzzy variables:	number of patches per plot; number of different land uses per plot; number of different disturbance types per plot; number of different frequencies per plot; number of different seasons per plot; number of different durations per plot; number of different sizes per plot; number of different forms per plot; number of different distributions per plot; number of different selectivities per plot
Land-uses (1/0):	forest; miscellaneous constructions; field; path; rock; settlement; transition zone; water body; fallow land/succession; grassland
Disturbances (1/0):	agriculture; biomass export; biomass input; breakage; clear felling; compaction (tracks); compaction (trampling); compaction (wheels); contamination; creek reallocation; collecting deadwood; dehydration; depression (water filled); erosion (water); excavation (open); farming; fencing; gardening; fire; flooding; foreign material; gravel (basalt); gravel (lime); grove felling; hydraulic engineering; leveling; macroherbivory; material storing; macroherbivory; mowing; none; nutrient input; pesticides; pond-drainage; quarry; rejuvenation; sealing; seeding; single tree felling; skidding track; soil/rock movements; thinning; wild boar; wood storage/movement
Frequencies (1/0):	1x/century; 1x/decade; 1x/year; 2x/year; 3x/year; >3x/year; steady diffuse; steady intense; none
Seasonalities (1/0):	quarter 1; quarter 1-3; quarter 1-4; quarter 1&4; quarter 2; quarter 2&3; quarter 2-4; quarter 3; quarter 3&4; quarter 4; none
Durations (1/0):	<1day; <1week; <1month; <1year; >1year; none
Sizes (1/0):	1/2-area; 1/4-area; 3/4-area; 4/4-area; linear/punctiform; none
Forms (1/0):	laminar; linear; punctual; none
Distributions (1/0):	heterogeneous; homogeneous; none
Selectivities (1/0):	age; location; species; age & location; age & species; age & species & location; species & location; lot-boundary; none

Since forests had a big influence of plant species richness at Grafenwöhr Training Area, I analyzed the different portions of forest cover on landscape level as well. Total area of forested patches within a plot of Frankenalb and Fichtelgebirge were calculated with ArcGIS. Analyses were conducted using the full data sets and reduced sets with pure open landscape data (0% forest) and pure forest data. For these forest data, 5% of non-forest portion was accepted which basically correspond to forest roads.

3.3.1 Ellenberg indicator values (and derived / calculated values)

Results of analyses with the Grafenwöhr data set on local (patch) scale showed a clear influence of abiotic parameters on local scale. For this reason the Ellenberg indicator values were included into the analyses of the three study sites (Ellenberg 1991). It was expected that the Frankenalb data show similar tendencies like Grafenwöhr because of the similar bedrock. Consequently, big differences of Fichtelgebirge data were likely. Ellenberg indicator values were derived from the databases BiolFlor (Version 1.1 - Klotz *et al.* 2002) and LEDA (Kleyer *et al.* 2008).

The parameters 'median', 'maximum', 'minimum', and 'standard deviation' were calculated for some Ellenberg values L (light), N (nutrients/nitrogen), F (soil moisture), R (pH), and S (salinity). These were named e.g., L.med; L.max; L.min; L.sd. The indicator values T (temperature), and K (continentality) were excluded according to Preston & Hill (1997). Basic requirement was the quantity of at least four values per indicator and patch. To prevent that single plant species on the outer end of the range would gain too much weight, the parameters were extended by the differences between the indicator values: 'maximum-minimum', 'maximum-median', and 'median-minimum' (e.g., L.maxmin; L.maxmed; L.medmin). Analyses on local scale were conducted for open landscape and forested patches.

3.3.2 Further parameters

In the multivariate statistics, approaches were included to test two common hypotheses in the open landscape. Several disturbance types and their time, space, and selectivity related characteristics were recorded. To test the **Intermediate Disturbance Hypothesis** (IDH), intermediate categories from the parameters 'frequency', 'duration', and 'size' were calculated, as these three stand for the intensity of a disturbance. These were 'once a year', 'twice a year' and 'three times a year' (=frequency), 'less than one week' and 'less than one month' (=duration), '50% of an area' and '75% of an area' (=size) (Table 3-4).

Table 3-4: Selection of parameters for testing the 'intermediate disturbance hypothesis'. Intermediate frequencies, durations and sizes were included

Parameters	Categories	Intensity
frequency:	>3x/y; steady intense/diffuse	high
	1x/y; 2x/y, 3x/y	intermediate
	1x/cent; 1x/decade; none	low
duration:	>1year; <1 year	high
	<1 week; <1 month	intermediate
	<1 day, none	low
size:	4/4 area	high
	1/2; 3/4 area	intermediate
	1/4 area, linear/punctual; none	low

Two different approaches of the indicator for intermediate disturbance were created:

1) Quantitative IDH (IDH-quant): each disturbance was assigned either a '1' for being in the intermediate category, or a '0' if not. IDH-quant is a sum of these values per patch. Since some patches have several disturbances, this value can exceed '1'.

2) Non-overlapping disturbance: To account for the multiple disturbances within a patch a second category was introduced: The outcompeting of intermediate disturbances. As an example we imagine a patch with two disturbances. One has an intermediate size and an intermediate frequency. Therefore we should include it into our analyses. However, the second disturbance shows a higher frequency and a larger size and belongs to the category high intensity. Therefore this disturbance overlaps the effect of the intermediate disturbance, which therefore was excluded.

Four values of the non-overlapping disturbance were included in the statistics:

- 'IDH 0': no intermediate disturbance in the patch
- 'IDH 1': one of the categories frequency, duration, and size in intermediate class
- 'IDH 2': two of the categories frequency, duration, and size in intermediate class
- 'IDH 3': all three categories frequency, duration, and size in intermediate class
- 'IDH x': patch with IDH 1-3, but with overlapping disturbance

To test the **Heterogeneous Disturbance Hypothesis** (HDH) (Warren *et al.* 2007), an indicator for the heterogeneity of the disturbance regime was needed. Fuzzy variables were calculated that counted the number of different parameters within a plot, i.e. land use, patch numbers, disturbance types, frequencies, etc. These variables were named 'number of different land-use classes (per plot)', 'number of different disturbance-types', etc. Table 3-5 shows the first four plots of Frankenalb (FA) as an example.

Table 3-5: Plots after adding fuzzy variables and species number (SR - alpha diversity), and quantitative fuzzy variables. Table shows four plots as example.

plot	SR	no.patches	no.diff.landuses	no.diff.disttypes	no.diff.freq	no.diff.seas	no.diff.dur
FA-A01	119	7	4	4	4	3	1
FA-A02	129	6	3	5	3	3	2
FA-A03	166	10	5	8	6	3	4
FA-A04	138	9	5	6	6	3	2

Furthermore, to avoid a patch-size effect on species richness, the species number per square meter was included, as well as the patch size. The following table (Table 3-6) shows all parameters additional to the ones for analyses on plot scale.

Table 3-6: Table of parameters for multivariate statistics on patch level, additional to the ones for analyses on plot scale.

Category	Variables
Ellenberg-Values:	L.min; L.med; L.max; F.min; F.med; F.max; R.min; R.med; R.max; N.min; N.med; N.max; S.min; S.med; S.max; L.maxmin; F.maxmin; R.maxmin; N.maxmin; S.maxmin; F.maxmed; N.maxmed
Intermediate Disturbance:	IDH x; IDH 0; IDH 1; IDH 2; IDH 3; IDH-quant

3.3.3 Multivariate statistics

Partial Least Squares Regression (PLS-R) was used to analyze the influence of the multiple variables on plant species richness and to filter and reduce the number of variables to the significant ones. A two step approach was conducted with a first analysis using the full set of parameters. A second analysis followed with significant parameters only, which were selected with the jack-knife function. The method is explained in detail in 2.3.

Beta diversity and species turnover (distance decay)

Beta diversity describes the similarity or dissimilarity of species in neighbouring plots. The Sørensen index (Sørensen 1948) is one of the most used indices to explain species similarity of two or more areas based on presence-absence data (Baselga 2010).

$$\beta_{sør} = 1 - \frac{2a}{2a + b + c}$$

With a: the number of shared species for Plots 1 and 2; b and c: the number of species that only appear on one of the two plots (i.e., b = number of unique species of Plot 1; c = number of unique species of Plot 2) and scaling between 0 (every species found in one plot is also found in the other plot) and 1 (no species in common) (Koleff *et al.* 2003; Ricotta & Burrascano 2008).

Distance decay analyses are used to calculate the relationship between the similarity in species compostion and its fate over distance (Nekola & White 1999; Soininen *et al.* 2007). Based on the Sørensen similarity, a distance decay analysis was conducted for open landscape plots, with a maximum proportion of 25% forest.

The significance of the results was assessed using Mantel tests with 1000 permutations (Legendre 1993); Spearman rank coefficient analysis was run for validation. For conducting the similarity analyses, the open source software R version 2.15.3 (R Core Team 2013) with packages ‘vegan’, version 2.0-10 (Oksanen *et al.* 2013) was used.

3.4 RESULTS

3.4.1 Bedrock & species richness

The three study areas differ in the bedrock. While Grafenwöhr Training Area and Frankenalb are situated on calcareous bedrock, the subsurface of Fichtelgebirge consists of siliceous phyllite. As a matter of fact the three study areas showed high differences in plant species richness both on plot and on patch scale. At Grafenwöhr Training Area, a total number of 647 plant species was recorded and at Frankenalb a number of 679 species. Whereas at Fichtelgebirge, situated on siliceous bedrock, only 407 plant species were recorded. These clear differences were also visible on plot level with a mean richness of nearly 150 species at Grafenwöhr, 110 plant species at Frankenalb and 61 species at Fichtelgebirge. However, on patch level these differences were not that clear at all anymore. While at in the semi-natural landscape of Grafenwöhr an average of 69 species per patch was found, the agricultural landscapes of Fichtelgebirge (22 species) and Frankenalb (28.4 species) did not indicate the disparity on larger scale. At Fichtelgebirge, 14 patches showed less than five and 74 patches less than ten species. At Frankenalb, 21 patches had less than five species; on 96 patches less than ten species were recorded. In both sites the minimum species numbers on patch scale were only one single species. At Fichtelgebirge an asphalted road facilitated only *Poa annua* as single species, whereas at Frankenalb, *Picea abies* was recorded as only species in a reforestation patch after clear felling. Minimum number of species per patch at Grafenwöhr was 18 (Table 3-7).

Table 3-7: Species richness (SR) at Grafenwöhr (semi-natural landscape), Frankenalb and Fichtelgebirge (both agricultural landscape). Displayed are total richness, mean richness on plot and patch level, and the variance of richness on both scales.

	SR	**Ø SR / plot**	**SR / plot (min-max)**	**Ø SR / patch**	**SR / patch (min-max)**
Grafenwöhr	647	148.3	66-298	69.0	18-178
Frankenalb	679	109.4	11-202	28.4	1-107
Fichtelgebirge	407	61.0	7-144	22.0	1- 61

3.4.2 The influence of land use on species richness

3.4.2.1 Agricultural landscapes

Partial Least Squares Regressions (PLS-R) were conducted to find out which parameters influence species richness on landscape scale of the agricultural landscapes. At Fichtelgebirge (Figure 3-4), parameters of heterogeneity but also of grassland (i.e. land use grassland, seasons 2&3, frequency 2x/year, size 4/ 4 area) and forest management (i.e. seasons 1& 4, rejuvenation, frequency 1x/decade) showed highest influence. At Frankenalb (Figure 3-5), mainly the fuzzy variables, indicating the heterogeneity of the landscape, showed the strongest prediction. Analyses showed a high correlation of 83% at Fichtelgebirge and 70% at Frankenalb. Results are further summarized in Table 3-8.

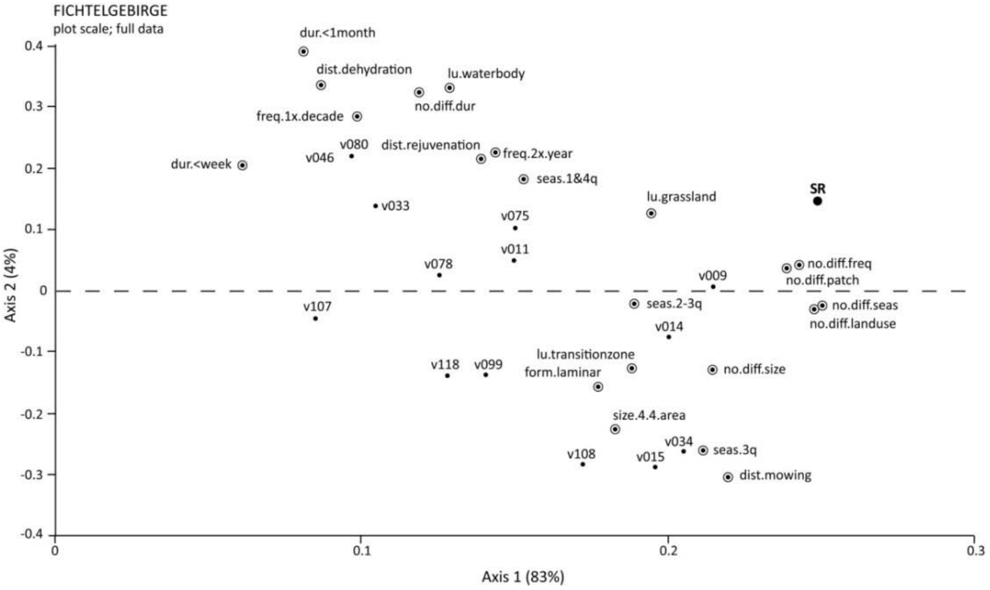


Figure 3-4: X- and Y-loadings of PLS-R. Analyzed were full Fichtelgebirge data on landscape level. Parameters related to heterogeneity, grassland management and forestry showed highest explanation. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

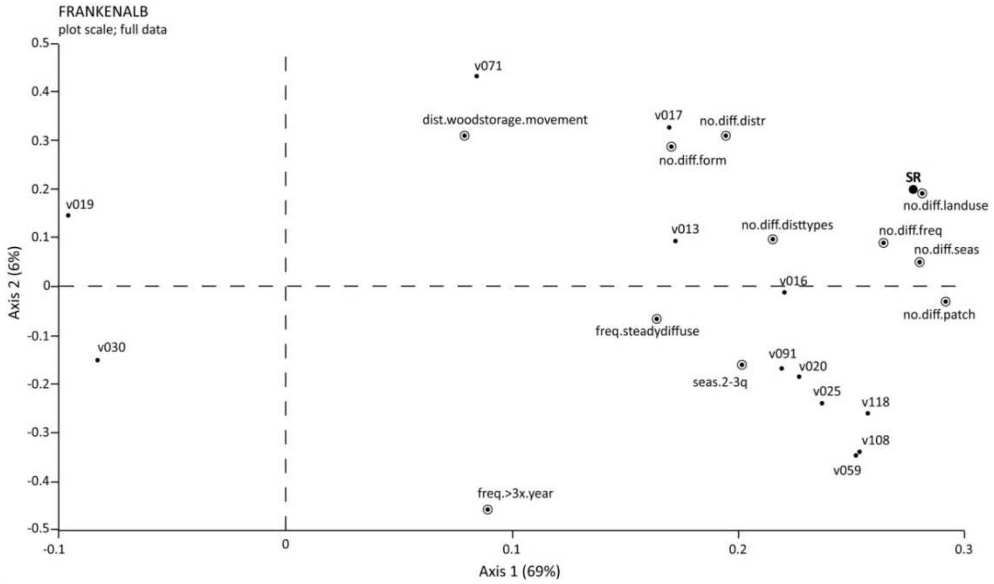


Figure 3-5: X- and Y-loadings of PLS-R. Analyzed were full Frankenalb data on landscape level. Parameters related to heterogeneity, grassland management and forestry showed highest explanation. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Table 3-8: Summary of results of Partial Squares Regression with full Fichtelgebirge (FG) and Frankenalb (FA) data on landscape level.

	N	No. parameters	R²	RMSE	RMSE [%]	No. variables	No. significant variables	No. PLS-R axes
FG	100	112	0.83	13	9.0	35	21	3
FA	100	112	0.70	24	11.9	24	11	3

Further analyses to force a reduction of parameters to a minimum without reducing the stability of prediction (see Buhk *et al.* 2007b), using several times the jack-knife function and selective deselection of parameters, ended in 15 most significant parameters at Fichtelgebirge and six parameters at Frankenalb. The highest positive influence was shown by the indicators for heterogeneity.

Based on this, the data sets were splitted into portions of forest cover to figure out the differences between forests and open landscapes. Six classes were formed and analyses were conducted with the forest covers 0% (open landscape), 0-25%, 26-50%, 51-75%, 76-100% and 100%. In contrast to the Grafenwöhr data of chapter two, an increasing portion of forest cover led to a decline in explanatory power and an increasing prediction error (Table 3-9).

Table 3-9: Subsets with 0%, 0-25%, 0-50%, 50-100%, 75-100% and 100% forest within one plot. The table shows PLS-R statistics and most significant positive and negative predictors for Fichtelgebirge (FG) and Frankenalb (FA).

	Forest cover [%]	**N**	**R²**	**RMSE**	**RMSE [%]**	**No. variables**	**No. significant variables**	**Explanation 1. axis [%]**
FG	0	46	0.77	12.5	11.1	20	14	77
	0-25	53	0.85	12.5	8.7	22	21	85
	0-50	58	0.83	12.6	8.8	25	24	83
	50-100	42	0.85	11.4	8.2	15	9	85
	75-100	33	0.73	11.2	11.7	8	4	73
	100	14	NA	NA	NA	NA	NA	NA
FA	0	19	0.82	16.9	9.2	31	31	86
	0-25	32	0.82	17.4	9.4	37	35	82
	0-50	44	0.73	20.5	10.1	35	34	73
	50-100	56	0.70	24.2	14.2	30	30	70
	75-100	45	0.68	24.5	14.6	22	22	68
	100	2	NA	NA	NA	NA	NA	NA

At Fichtelgebirge, the power of the model was high with an explanation of 77% ($R^2=0.77$, RMSE=12.5 ≙ 11.1%). However, only 14 significant variables were left after the two runs on PLS-R. The heterogeneity of land uses, and frequencies, seasons and durations of disturbances showed highest influence (Figure 3-6).

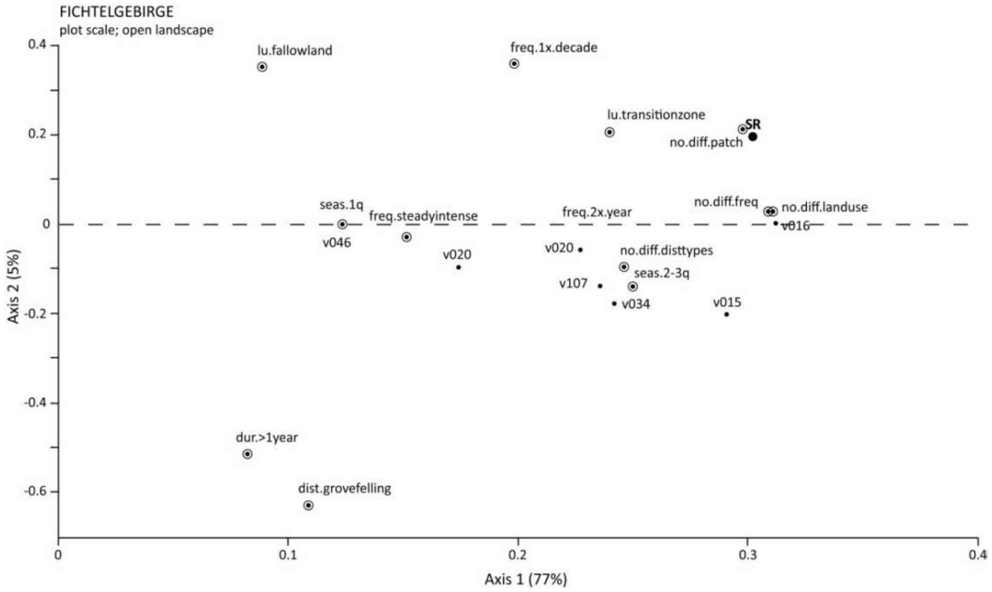


Figure 3-6: X- and Y-loadings of PLS-R. Analyzed were Fichtelgebirge open landscape data (0% forest) on plot scale. Analyses showed a high correlation of 79% with the 14 most significant parameters. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

At Frankenalb, 32 significant parameters were left after two statistical runs. Power of explanation was high ($R^2=0.80$) and RMSE low (16.9 ≙ 9.2%), but did not differ much from Fichtelgebirge analysis. Two parameters were obviously negatively correlated. These were the land use ‘field’ and the directly related disturbance ‘agriculture’. Mainly the fuzzy variables indication a heterogeneous disturbance and land use regime were the dominant explanatory variables (Figure 3-7).

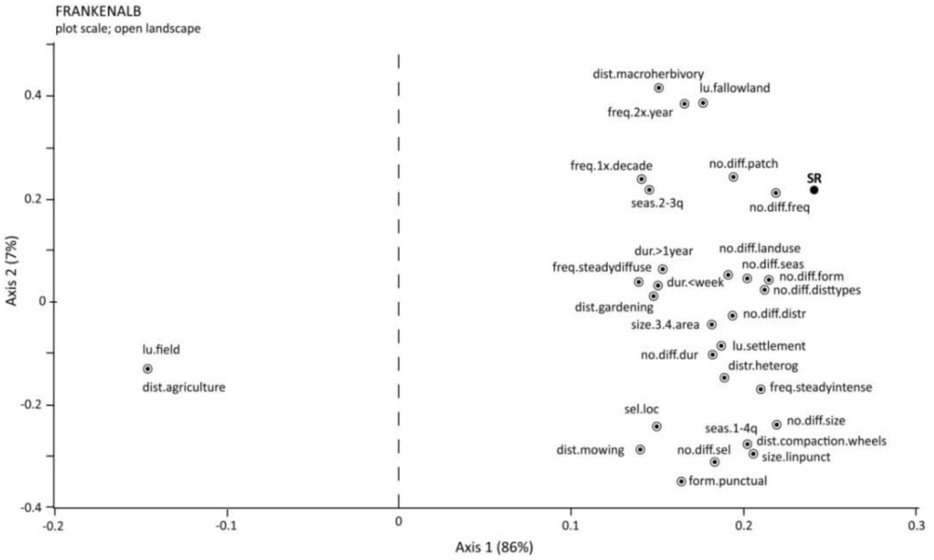


Figure 3-7: X- and Y-loadings of PLS-R. Analyzed were Frankenalb open landscape data (0% forest) on plot scale. Analyses showed a high correlation of 80% with the 31 most significant parameters. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Contrary to our expectations, the agricultural landscapes showed some influence of heterogeneity, especially the study area of Frankenalb. Therefore, a closer look at the correlation between the number of land-use types per plot and species richness (SR) and the number of patches per plot and species richness, respectively, was conducted.

The linear regressions that calculate the correlation between the number of land-use types in a plot and species richness, showed significant results for both study sites (FA: 66%, Figure 3-8, left; FG: 67%, Figure 3-8, right).

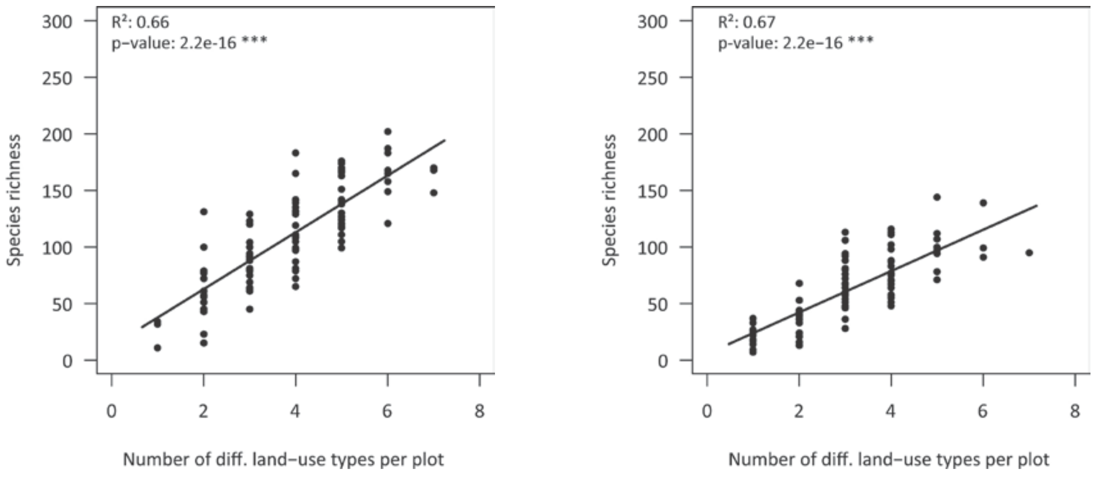


Figure 3-8: Linear regressions of the number of land-use types within a plot and species richness at Frankenalb (FA, left) and Fichtelgebirge (FG, right). Results show a significant correlation (R²) of 66% (FA) and 67% (FG).

Plots were subdivided into patches according to their land use and disturbance regime. Therefore, regressions using the number of patches within a plot correlated with species richness should result in a similar picture like the regressions above. Indeed, results showed an even higher prediction of 50% at Frankenalb (Figure 3-9, left) and 69% at Fichtelgebirge (Figure 3-9, right).

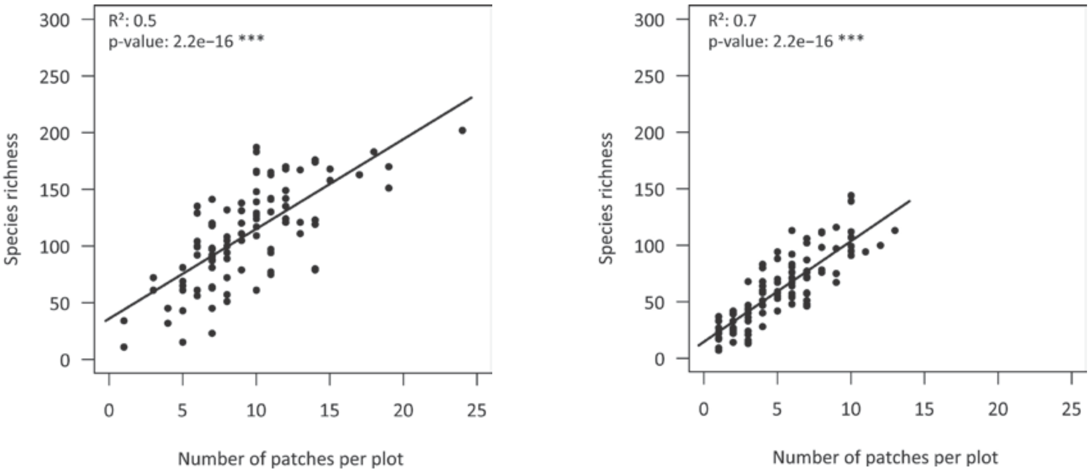


Figure 3-9: Linear regressions of the number of patches within a plot and species richness at Frankenalb (FA, left) and Fichtelgebirge (FG, right). Results show a significant correlation (R²) of 50% (FA) and 69% (FG).

3.4.2.2 Agricultural versus semi-natural landscapes

The following analyses were conducted to directly compare the agricultural landscapes with the semi-natural landscape. Above displayed results showed, that the agricultural landscape had some tendency towards a heterogeneous landscape, especially at Frankenalb. Results in chapter two showed a high heterogeneity of the semi-natural landscape.

PLS-R was conducted with all three datasets at once. Three different analyses were done, using (I) the full amount of plots (N=300), (II) only open landscape plots (no forest at all, N=121) and (III) only forest plots, allowing 5% for forest roads (95-100% forested, N=22). All three analyses showed a high explanation power between 77% and 79%.

Looking at the result of the full data (FIG) showed a clear visible pattern of heterogeneity on the first axis (77% explanation). Disturbances play a more important role on the second axis, but with a poor explanation of only 4%.

The three study sites that were added as categorical variables, showed very different tendencies along the axes. Species richness was explained mainly by the heterogeneous parameters. The variable 'Grafenwöhr' was placed closest to this section. On the opposite site of the first axis Fichtelgebirge pulled into the negative but significant direction, indicating a dependency of disturbances related to forestry. In between, the category Frankenalb was not indicated as significantly relevant.

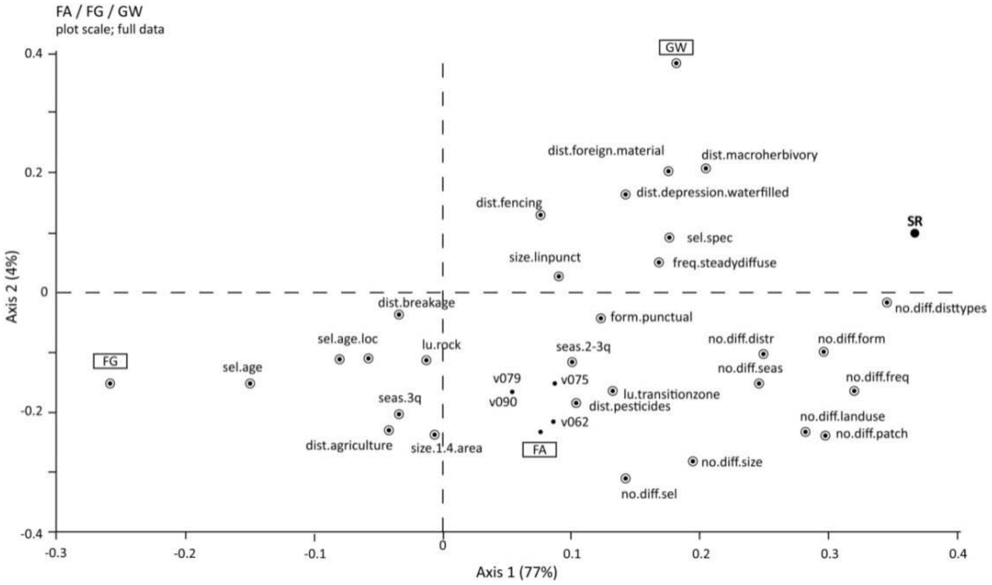


Figure 3-10: X- and Y-loadings of PLS-R. Analyzed were full data of Frankenalb, Fichtelgebirge and Grafenwöhr on landscape level. Species richness was explained mainly by the heterogeneous parameters. 'Grafenwöhr' showed a significant positive correlation, whereas Fichtelgebirge showed negative but significant correlation, indicating a dependency of disturbances related to forestry. In between, the category Frankenalb was not indicated as significantly relevant. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

'Open landscape plots' indicate that within the certain plots there is no patch related to the land use 'forest'. Nevertheless, we might find trees and therefore forestry related disturbances as well, for example in a transition zone between a forest and the surrounding open matrix. The analysis with the 121 entirely open plots showed again the opposed direction between Grafenwöhr and Fichtelgebirge along the first axis. Once more, Frankenalb was not significant. Along with the negative correlation of Fichtelgebirge went all disturbances related to agriculture. Positively correlated were again parameters concerning the heterogeneity of the disturbance regime and smaller scaled (linear, punctual) and short-termed disturbances (Figure 3-11).

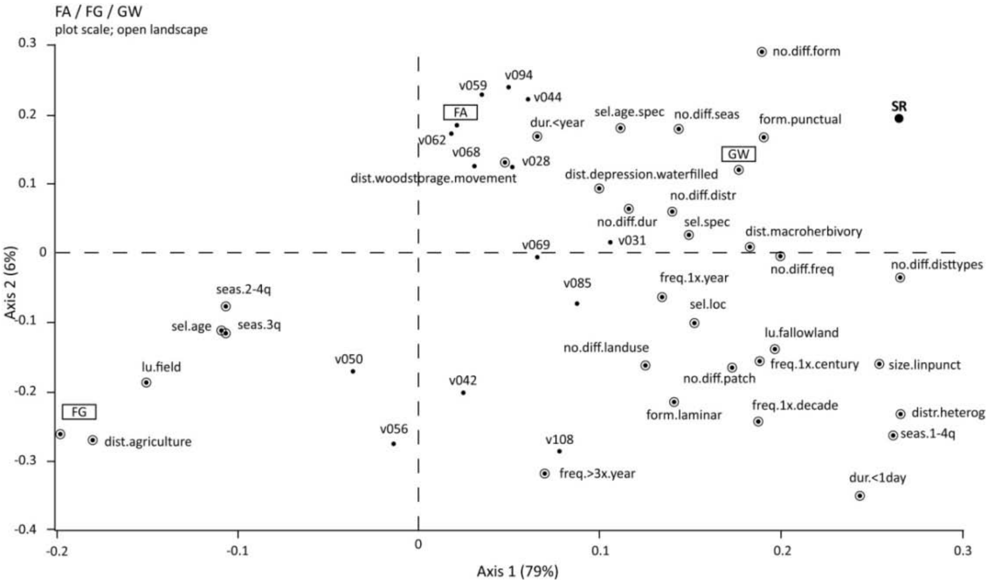


Figure 3-11: X- and Y-loadings of PLS-R. Analyzed were open landscape plots of Frankenalb, Fichtelgebirge and Grafenwöhr on landscape level. Positively correlated were parameters concerning the heterogeneity of the disturbance regime and smaller scaled (linear, punctual) and short-termed disturbances. Negatively correlated were parameter related to agricultural land use. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

A further analysis was conducted with forested plots only (Figure 3-12). However, to consider roads that intersect the forests, the area covered by forest with in a plot was set by 95-100%. Grafenwöhr and Fichtelgebirge showed again opposite influence, Frankenalb showed no significant effect. Results of the three analyses are summarized in Table 3-10.

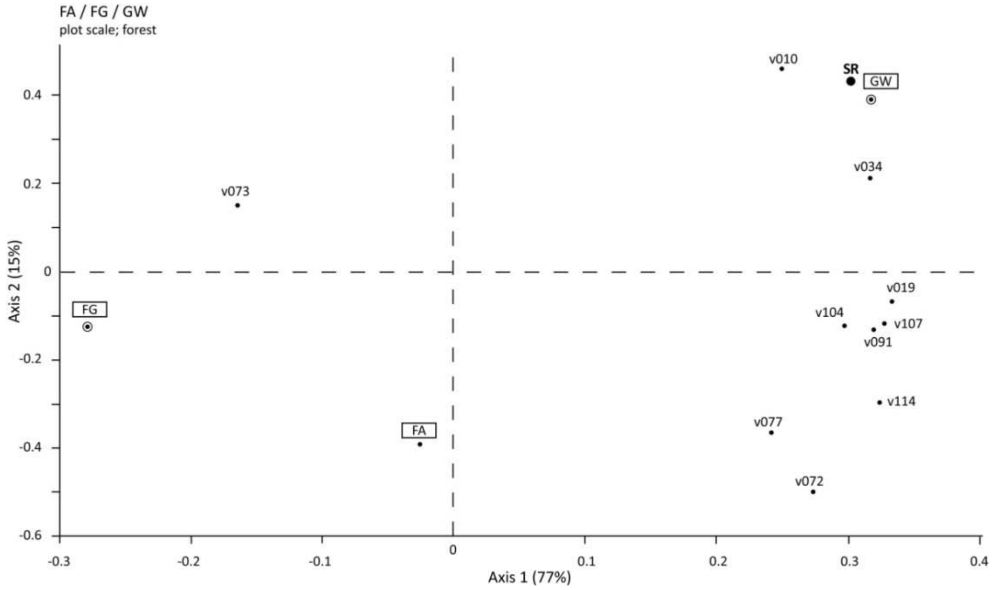


Figure 3-12: X- and Y-loadings of PLS-R. Analyzed were forested plots (95-100% forest to consider forest tracks) of Frankenalb, Fichtelgebirge and Grafenwöhr on landscape level. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Table 3-10: Results of PLS-Rs with the joint data of Grafenwöhr, Frankenalb and Fichtelgebirge on landscape scale. (I) Full data, (II) only open landscape plots (0% forest) and (III) only fully forested plots (95-100% forest).

	N	R²	RMSE	RMSE [%]	No. variables	No. significant variables	Explanation 1. axis [%]
(I) Full	300	0.79	24.1	8.1	35	30	77
(II) Open landscape	121	0.77	20	9.2	47	33	79
(III) Forest	22	0.90	15.6	9.0	15	10	87

The quality of explanation rose with the amount of forest within the plots. This is controversial to the results of analyzing Frankenalb and Fichtelgebirge separately, but supports the results of the analyses of Grafenwöhr data only. At Grafenwöhr forests contain a total of 489 plant species and a mean of 84.7 species per patch. At Fichtelgebirge, 199 species with an average of 18.5 species per patch showed a pretty poor result. At Frankenalb species number was 418 with an average of 25.7, and therefore a high total number but the average values on intermediate level (Table 3-11).

Table 3-11: Mean and total species richness at Grafenwöhr, Frankenalb and Fichtelgebirge per land-use type.

Total species richness	**Forest**	**Grassland**	**Field**	**Fallow land**	**Transition zone**	**Settlement**	**Rock**	**Path**	**Water body**
Grafenwöhr	489	349	0	529	423	240	0	376	345
Frankenalb	418	305	222	345	490	301	31	403	42
Fichtelgebirge	199	224	122	121	284	139	68	203	174
Mean species richness	**Forest**	**Grassland**	**Field**	**Fallow land**	**Transition zone**	**Settlement**	**Rock**	**Path**	**Water body**
Grafenwöhr	84.7	71.3	0	69.1	60.4	64.5	0	56.5	53.6
Frankenalb	25.7	30	21.3	35.7	34.2	44.8	31	22.1	15
Fichtelgebirge	18.5	27.4	18.2	30.7	27.2	30.1	20.4	16.8	22.8

A combined regression including all three study sites for the correlation between 'number of land-use types per plot' and 'number of patches per plot' with species richness show the same order of our study sites in the regressions (Figure 3-13), like in the multivariate analyses. Remarkably, the two agricultural landscapes have similar low species numbers (y-axis) at low heterogeneity (x-axis), but Frankenalb showed a higher increment with increasing heterogeneity.

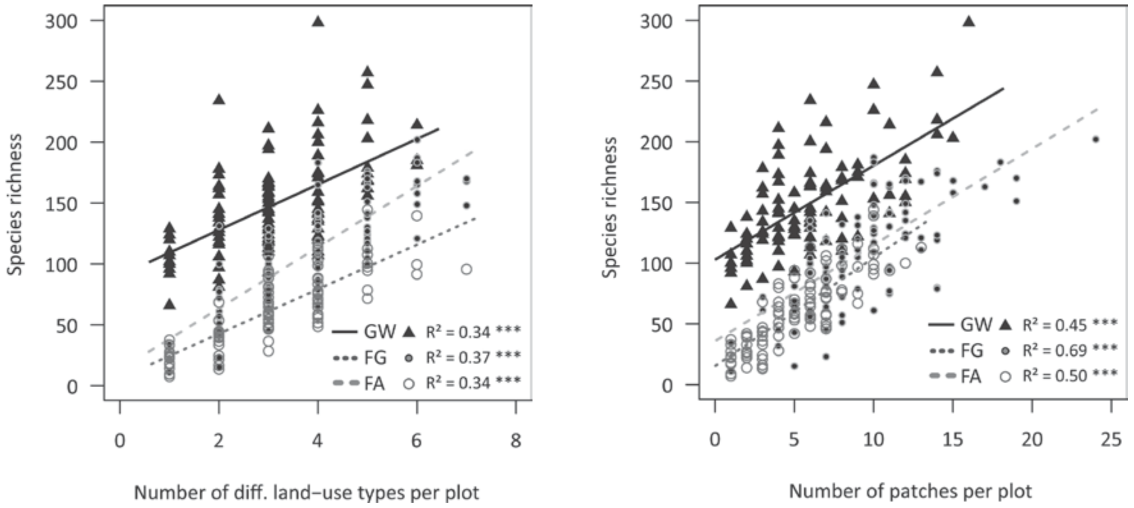


Figure 3-13: Linear regressions of the three data sets, correlating species richness with number of different land-use types per plot (left) and species richness and number of patches per plot (right). Result show that both agricultural landscapes have identical species richness at low heterogeneity. Frankenalb showed higher increment with increasing heterogeneity.

3.4.3 The influence of the disturbance regime

For each patch the disturbance regime was recorded. Most patches showed more than one disturbance. For example, when a meadow is mowed, we find the mowing itself, but also the linear compaction of the soil because of the tractors wheels. Furthermore, several meadows are fertilized. On plot level, the number of different disturbance types was added and correlated with the plant species richness (gamma diversity on plot level).

The regressions show that an increasing number of disturbance types cause an increasing species richness within a plot (Figure 3-14). This was relevant for all three study sites. Since we calculated with the number of different disturbance types, this is an indicator for the heterogeneity of the disturbance regime. In fact, plots with only one disturbance show the lowest species richness and therefore are indicators for homogeneity. At Grafenwöhr, we found 35 different disturbance types (max. 14 different disturbances in one plot), at Frankenalb we found 25 (max. 10 per plot) and at Fichtelgebirge 21 (max. 9 per plot). Especially at Grafenwöhr, natural and anthropogenic disturbances were overlapping.

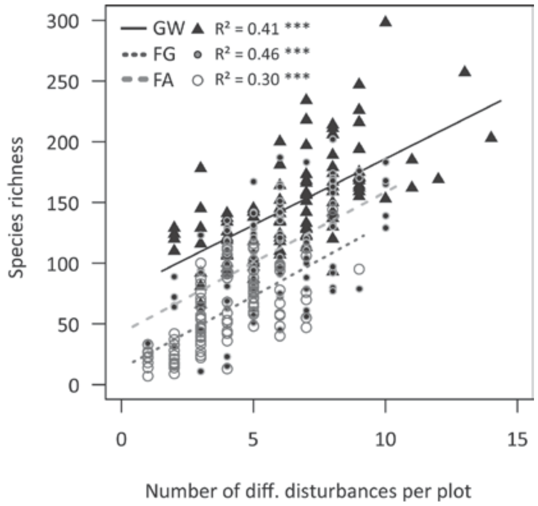


Figure 3-14: Linear regression of the three data sets, correlating species richness with number of different disturbances per plot. Regressions show the positive influence of a multiple disturbed landscape on plant species richness.

3.4.4 Analyses including Ellenberg indicator values on patch scale

The analyses conducted so far at Grafenwöhr (chapter two) and on landscape level with all three data sets showed two clear results. First, the differences between forests and open landscapes were that big that they have to be analysed separately. Second, adding abiotic factors at Grafenwöhr on local scale significantly enhanced the explanation power.

Conducting a PLS-R with the **open landscape** data of Fichtelgebirge resulted in the highest significance of the abiotic parameters N (nutrients), R (pH) and F (humidity). They spanned the first axis from the far positive (variances of abiotic factors) to the far negative (minimum value of N). The overall explanation power was only 55% with 32 significant parameters (Figure 3-15).

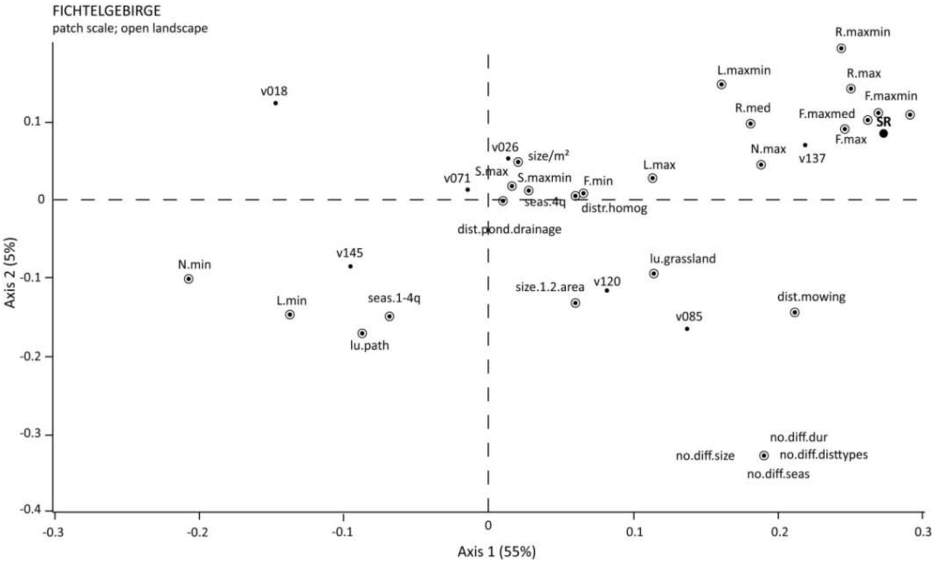


Figure 3-15: X- and Y-loadings of PLS-R. Analyzed were Fichtelgebirge data in the open landscape at patch level. Abiotic parameters N, R, and F showed highest influence. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Analyses at Frankenalb showed a similar picture: the variances of the abiotic parameters N (nutrients), R (pH) and F (humidity) showed highest explanation for species richness. Strongest negative influence had the minimum values of nitrogen and humidity (Figure 3-16).

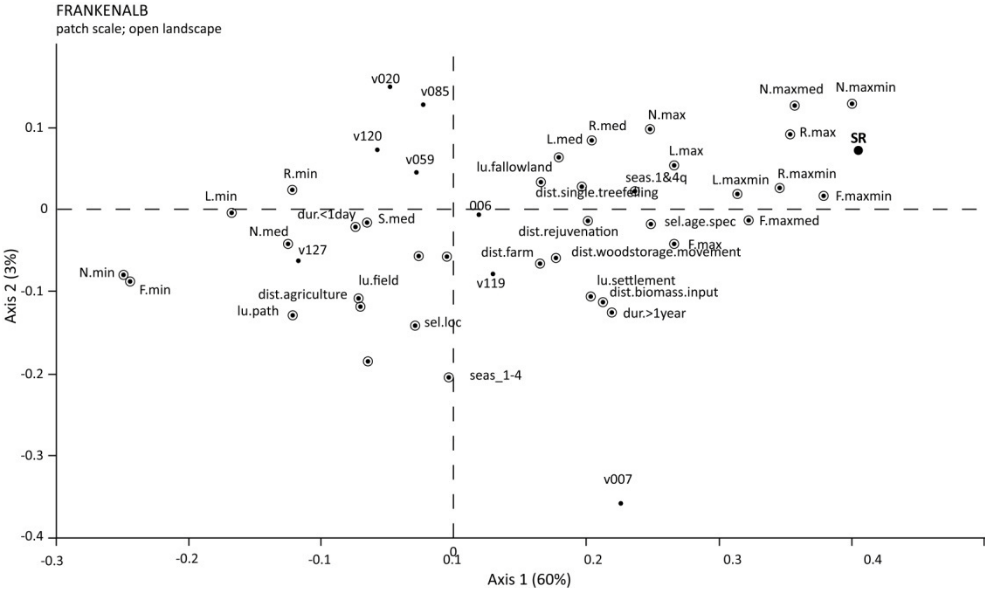


Figure 3-16: X- and Y-loadings of PLS-R. Analyzed were Frankenalb data in the open landscape at patch level. Abiotic parameters N, R, and F showed highest influence. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Multivariate analyses in the **forest** data of Fichtelgebirge resulted in the significant variances of nitrogen (N.maxmin), humidity (F.maxmin) and pH (R.maxmin). Negatively correlated was the punctual disturbance form (Figure 3-17).

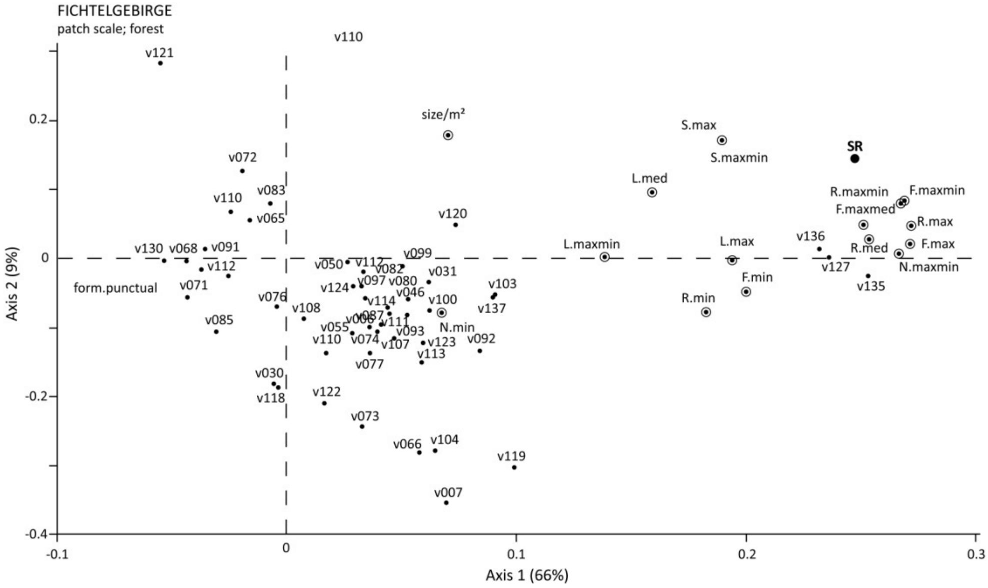


Figure 3-17: X- and Y-loadings of PLS-R. Analyzed were Fichtelgebirge data in forests at patch level. Abiotic parameters N, R, and F showed highest influence. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Forests at Frankenalb contain a total of 418 plant species. Besides the maximum pH values (R.max), the variances of nitrogen (N.maxmin), light (L.maxmin) and humidity (F.maxmin) show the highest positive influence on species richness on the first axis. A negative effect show the minimum values of humidity (F.min) and light (L.min) (Figure 3-18).

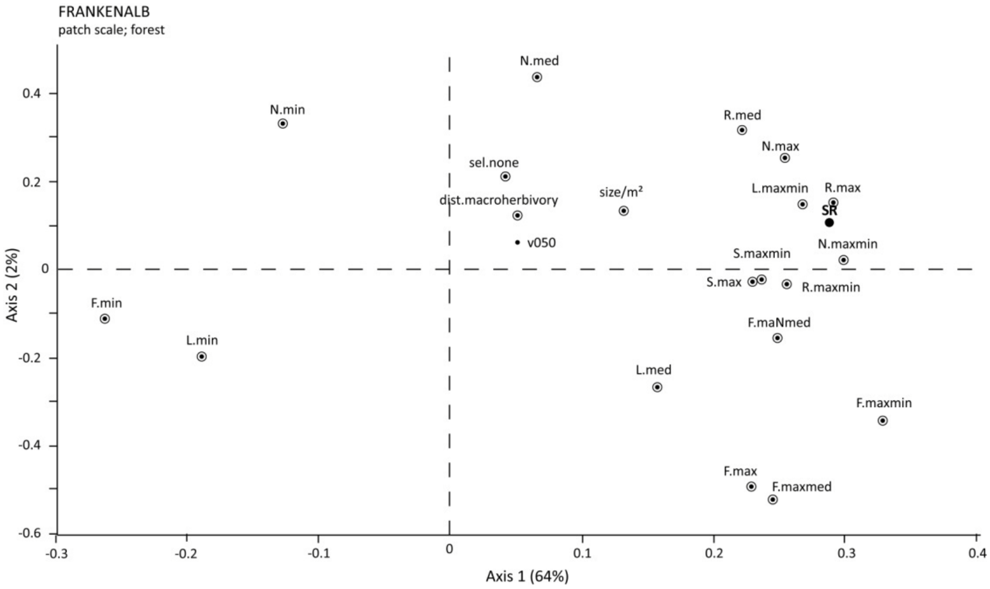


Figure 3-18: X- and Y-loadings of PLS-R. Analyzed were Frankenalb data in forests at patch level. Abiotic parameters N, R, L and F showed highest influence. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

3.4.5 Comparison of agricultural and semi-natural landscapes on patch scale

A PLS-R including all three data sets showed opposite effects of the landscapes. In this analysis the three study sites were included as fuzzy variables to indicate their relation to high species richness when included in a single analysis.

The first analysis was conducted with the full data set and 2043 patches in total. Like on plot scale, the semi-natural landscape was strongly related to species richness. While on plot scale the less intense agricultural landscape of Frankenalb showed an intermediate effect on species richness, on patch level analyses resulted in a similar strong negative effect as Fichtelgebirge. Individually viewed, the three study sites landscapes a most significant influence of nitrogen, pH and humidity. However, in combination only humidity and nitrogen showed the biggest effect, both in positive and negative direction. Positively correlated were their variances (F.maxmin, N.maxmin). Negatively correlated were their minimum values (Figure 3-19).

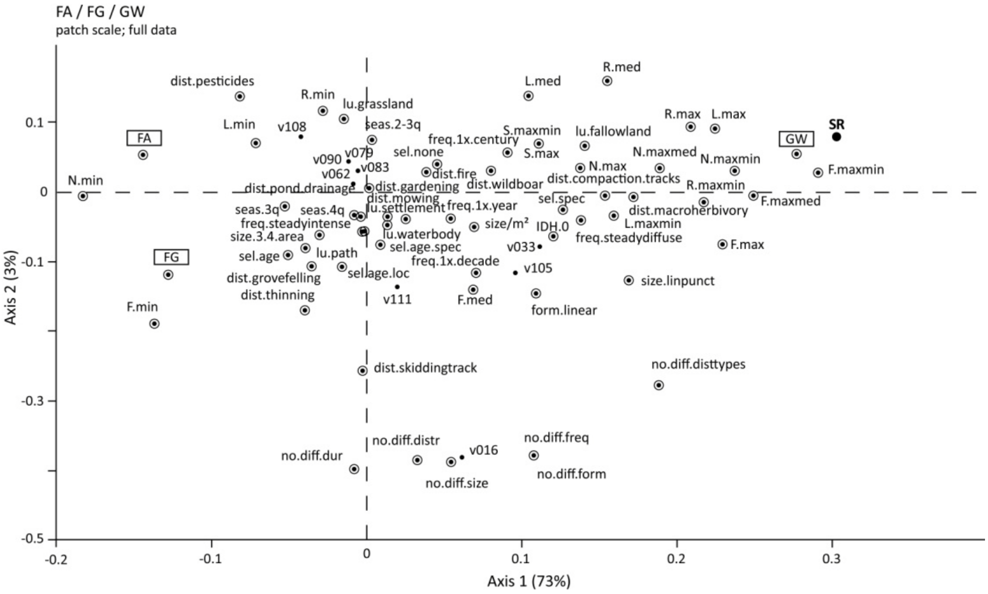


Figure 3-19: X- and Y-loadings of PLS-R. Analyzed were full data of all three data sets at patch level. Variances of the abiotic parameters F, R and N showed highest influence. Grafenwöhr was positively correlated, whereas both agricultural landscapes showed significant negative correlation. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Analyses with open landscape (1579 patches) and forests (464 patches) showed the same presentation of the three study sites like in the full data. However, most positive effect in the open landscape had the variances of humidity (F.maxmin) and light (L.maxmin). Most negative effect had the minimum values of nitrogen (N.min) and humidity (F.min). In second row the agricultural land use (i.e., 'land use field', 'disturbance agriculture', 'season 2nd-4th quarters') showed the low species numbers in fields (Figure 3-20).

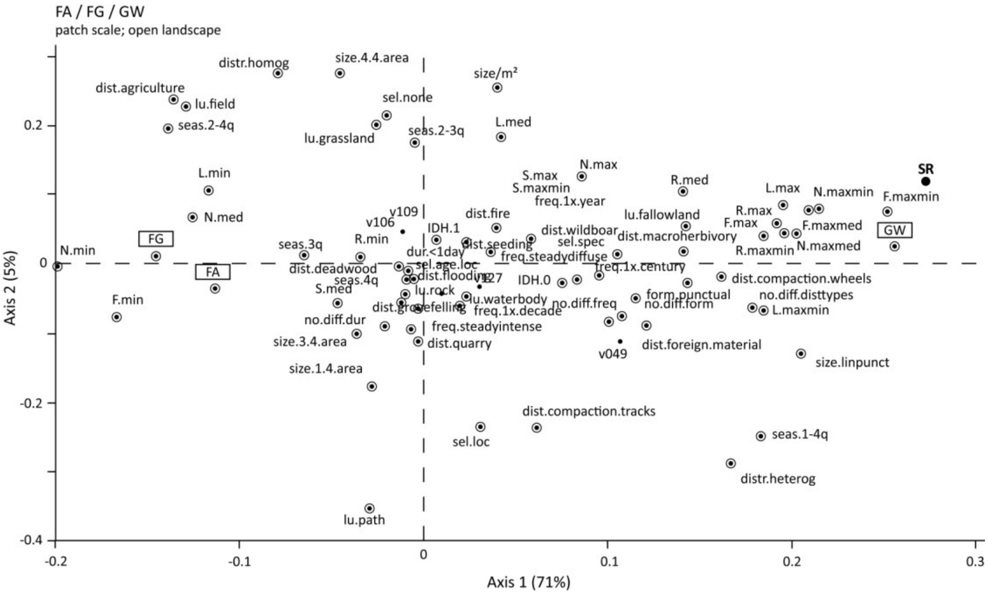


Figure 3-20: X- and Y-loadings of PLS-R. Analyzed were open landscape data of all three data sets at patch level. Variances of humidity (F) and light (L) showed highest positive correlation. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

In forests, also the variances of humidity (F.maxmin) and the maximum values of light (L.max) showed the highest prediction for specie richness (Figure 3-21). At the negative end were the minimum values of nitrogen (N.min) and light (L.min).

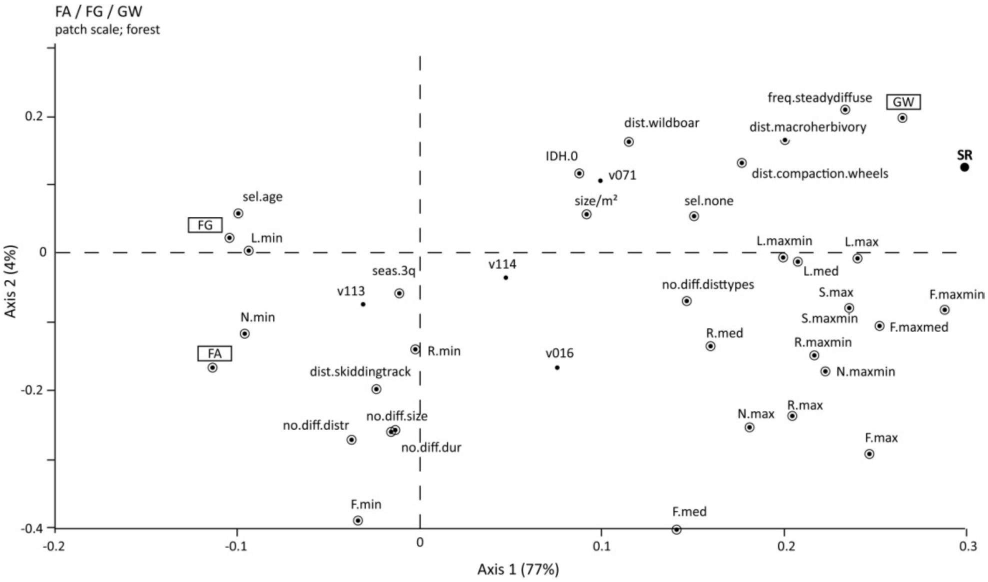


Figure 3-21: X- and Y-loadings of PLS-R. Analyzed were forest data of all three data sets at patch level. Variances of humidity (F) and nitrogen (N) showed highest positive correlation. Named variables indicate significant correlation, coded variables indicate non-significant variables. For description of variables see supplement S1.

Both regressions showed area as significant for species richness, but with a lesser explanation than abiotic parameters. A separate analysis revealed a strong correlation between the patch sizes in the semi-natural landscape, whereas the agricultural landscapes did not show a significant correlation (Figure 3-22).

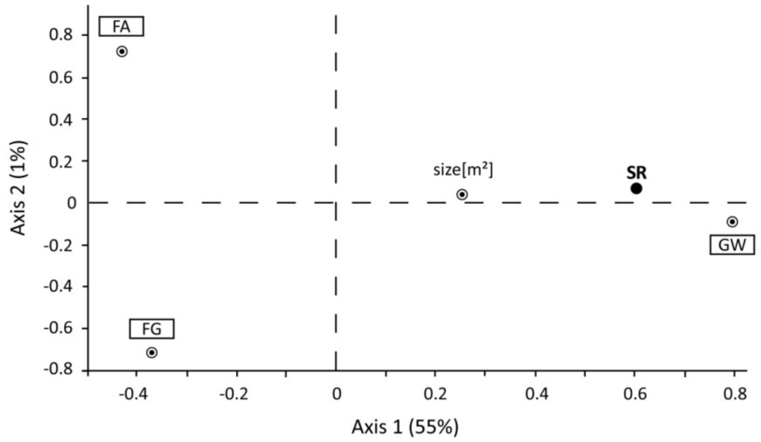


Figure 3-22: X- and Y-loadings of PLS-R. Grafenwöhr (GW) showed a positive correlation to species richness and area effect, whereas the agricultural landscapes where negatively correlated.

3.4.6 The common hypotheses IDH and HDH

For testing the IDH, different parameters were included in the multivariate analyses (see methods chapter 3.3.2). However, the question of any sign concerning the Intermediate Disturbance Hypothesis could not be answered with PLS-R. The variables were eliminated during the reduction of parameters.

A separate regression was conducted, including patch size, species richness and quantitative IDH. Background was the assumption that a larger area shows a higher probability of disturbances within the intermediate range, and therefore agreeing with the IDH. The analysis resulted in a significant positive (GW) and a tendentious positive (FG, FA) correlation between species richness and patch size in all three data sets. However, the IDH showed a different picture. The regression between species richness and size of the patch shows a positive correlation at GW. Also the IDH showed a weaker but still positive correlation. This means, the larger the patch size the more species occur. At Frankenalb we see a weaker but still positive correlation between the size of a patch and species richness. However, the intermediate disturbance shows nearly no dependency on area. Also at Fichtelgebirge we find a correlation between the size of a patch and species richness. But here the IDH is significantly negative correlated to the area. Results are summarized in Table 3-12.

Table 3-12: Correlations between patch size, species richness and IDH at Grafenwöhr, Frankenalb and Fichtelgebirge.

	Patch size	Species richness	IDH quant
Grafenwöhr	↑	↑	↗
Fichtelgebirge	↑	↗	↓
Frankenalb	↑	↗	→

3.4.7 Beta diversity and species turnover

The data of Frankenalb showed big differences between total species numbers at landscape scale (γ-diversity) and species richness at patch scale (α-diversity). In comparison, Grafenwöhr, based on the same bedrock, showed high species numbers on both scales. In order to detect difference in β-diversity, Sørensen similarity was calculated for open landscape plots with a maximum of 25% forest (Figure 3-23). The military training area showed a mean similarity of 0.45, the extensive agricultural landscape of Frankenalb 0.4, and the intense agricultural landscape of Fichtelgebirge 0.39, respectively.

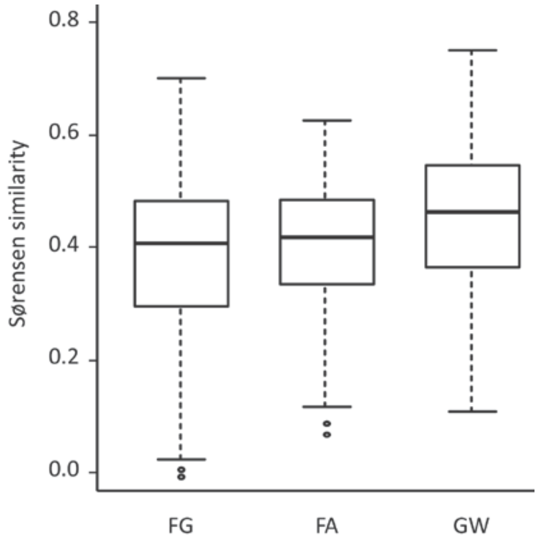


Figure 3-23: Boxplots of Sørensen similarity of the semi-natural landscape (GW), the extensive agricultural landscape (FA) and the intensive agricultural landscape (FG) in open landscape (max. 25% forest) show different similarities, as it is GW>FA>FG.

The distance decay analysis revealed different decays of the three landscapes (Figure 3-24). Here, the military training area showed the steepest slope of the linear regression (i.e., species turnover in a closer distance), the intense agricultural landscape showed nearly no decay. At Fichtelgebirge, very low similarities (up to full dissimilarity) were calculated.

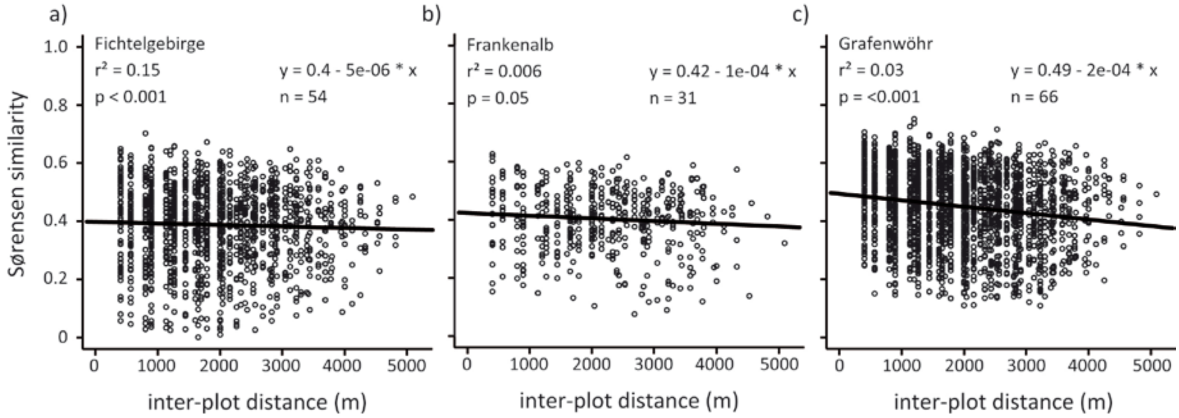


Figure 3-24: Inter-plot distance to similarity relationship (distance decay), based on Sørensen similarity analyses in open landscape plots with max. 25% forest at GW, FA and FG, show a higher decay at the semi-natural landscape.

3.5 DISCUSSION

Results showed a nearly similar high overall species richness at Frankenalb and Grafenwöhr. At Fichtelgebirge, only approximately two third of species were found. Frankenalb and Grafenwöhr have in common that both are situated on calcareous bedrock, whereas Fichtelgebirge is situated in siliceous bedrock. Land use and disturbance regime are comparable between Fichtelgebirge and Frankenalb, but intensity is higher at Fichtelgebirge. Several studies support the hypothesis of species rich landscapes on calcareous substratum (e.g., Ewald 2003; Marini *et al.* 2008; Mijangos *et al*. 2010). Some studies even compare both calcareous and siliceous bedrock and prove the differences in species richness (e.g., Pausas & Carreras 1995; Jentsch 2001; Michalet *et al.* 2002). Besides the bedrock, further factors are named in the scientific literature, which influence species richness. These are for example the elevation (e.g., Bhattarai & Vetaas 2003) and the aspect (exposition) (e.g., Lieffers & Larkin-Lieffers 1987) of a study site. Frankenalb and Grafenwöhr were sampled in identical elevations between 400 m and 580 m a.s.l., but where exposed to different directions (FA: north-east, GW: south). Fichtelgebirge was located at higher elevation (600 m-700 m) and south-east exposed, which surely is a disadvantage comparing to the other data sets. However, the gradients in these additional factors have to be bigger to be counted for a significant change. Therefore, the expectation that bedrock is the most important driver was met.

H2) Land use (agric. vs. semi nat.) is second most important

Multivariate statistics concerning the influence of land use on species richness gave different results for the three study sites. The separate analyses of the agricultural sites showed that at Fichtelgebirge, grassland had a significant positive influence on species richness, whereas at Frankenalb, fields were negatively correlated. Species richness at Fichtelgebirge was very low, apart from grasslands and transition zones. The latter played a tangential role because of its small area, but the ten times larger area of grassland was well represented in the analysis. Since species richness was the response variable and grassland showed high values in comparison with the other land-use types, this land use was marked as highly significant, despite the standardization. Correspondingly at Frankenalb, fields showed a significant negative correlation. Total species richness of several land-use types was very high on this site, but not on fields. Hence, the discrepancy was visible in the results. At the military area, forests and fallow land had highest species richness. Even in the combined calculations, including all three data sets, the importance of forests at Grafenwöhr was visible.

Besides these individual prominent land-use types, the heterogeneity of the land use, included as ‘number of different land uses’, consistently showed highest explanation. My results correspond with a cross-European study in agricultural landscapes (Billeter *et al.* 2008) and the hypothesis validated.

H3) In the semi-natural landscape, the overlapping anthropogenic and natural disturbances lead to a high heterogeneity as compared to the agricultural landscapes

Disturbances play an important role in ecosystem dynamics; I differentiated between natural and anthropogenic disturbances. Natural disturbances are seen to enhance biodiversity (e.g., Grubb 1977; Huston 1979), whereas anthropogenic alteration reduces species richness and abundance. Ernoult *et al.* (2003) stated that the human impact more and more replaces natural disturbances. One characteristic of a semi-natural landscape is that the human influence does not affect all areas and therefore gives space for natural processes. Consequently, it was expected to find more natural disturbance types at the semi-natural landscape of Grafenwöhr Training Area. However, there was no difference between the number of different natural disturbance types, but a big difference in their appearance. In the agricultural landscapes, natural disturbances like tracks and gnaw marks by macroherbivores or broken branches by wind were rare.

At the semi-natural landscape, natural disturbances were damages of the vegetation cover and top soil by wild boar, tracks and gnawed buds by deer and damaged trees due to wind breakage. Especially the damages by deer were omnipresent. Their traces were found on one third of the patches. These natural disturbances often overlap with anthropogenic disturbances in the semi-natural landscape and influence species richness in a positive way (Warren *et al.* 2007). Since many patches were influenced by more than one disturbance type, the factor between the number of patches in a plot and the recorded disturbance types was calculated. This factor indicates the heterogeneity of a disturbance regime. At the semi-natural landscape, an average of 2.4 disturbance types per patch was recorded. In the agricultural landscapes the factors were 1.5 at Frankenalb and 1.4 at Fichtelgebirge, respectively. The number of overlapping disturbances correlates with the species richness of a site. Therefore, the hypothesis was validated.

H4) Disturbance type is less important than the combination of various disturbances at plot (landscape) and patch (local) scale

However, the result that overlapping disturbance types enhance species richness does not meet the assumption, that a certain disturbance type is relevant for species richness. Most meaningful and significant on plot scale was the combination of various disturbances, indicated by the fuzzy variables "number of ...". This result is highly significant for the semi-natural landscape and Frankenalb. However, at Fichtelgebirge this effect seems to be weaker. There, disturbances and disturbance combinations related to grassland showed second highest influence after the heterogeneity of the disturbance regime. In a recently published study, Buma & Wessman (2012) found that not the simple number of disturbances has the higher explanation of species richness, but the types and combinations of disturbance types. However, they leave undefined, what the parameters for an additive effect are.

In multiple regressions with species richness as dependent variable, more weight is given to these species-rich patches. The comparison of the two agricultural landscapes showed a nearly similar proportion of grassland patches within the open landscape (19.2% at Frankenalb, 21.4% at Fichtelgebirge). However, at Fichtelgebirge the most species rich habitat with a major extent was grassland with an average of 27.4 plant species per patch. The lowest species richness was found in fields that contained an average of 18.2 plant species and which showed a significant negative effect in the analyses (land use field, disturbance agriculture).

Furthermore, these results show differences between the two agricultural landscapes regarding their land-use intensity. Both study sites were sampled using a grid of 100 plots of one hectare size. At Frankenalb 924 patches were allocated to the land-use and disturbance system, nearly twice as many as at Fichtelgebirge (524 patches). Fieldwork was conducted in two different years but by the identical person in charge, which reduces the error to a minimum. This suggests that the more intense agricultural land-use at Fichtelgebirge leads to a homogenization of the landscape with a reduced number of smaller patches. The average patch size of 1915.4 m^2 at Fichtelgebirge and 1082.3 m^3 at Frankenalb proves this suggestion.

With this background the results of hypothesis 1 and 2 appear in a different light and have to be qualified. Actually, species richness of a landscape predominantly can be traced back not only to the different bedrock, but also to the land use. The agricultural impact at Fichtelgebirge is higher than at Frankenalb, where land use is more extensive. The comparable high species richness of Grafenwöhr and Frankenalb, which was related to the similar bedrock, might be much lower at Frankenalb in case of an identical intensive agricultural impact like we find at Fichtelgebirge. Hence, the question arises if the high species richness of Frankenalb has to been seen as an artefact of the lower land-use intensity and is not caused by the calcareous bedrock (Figure 3-25).

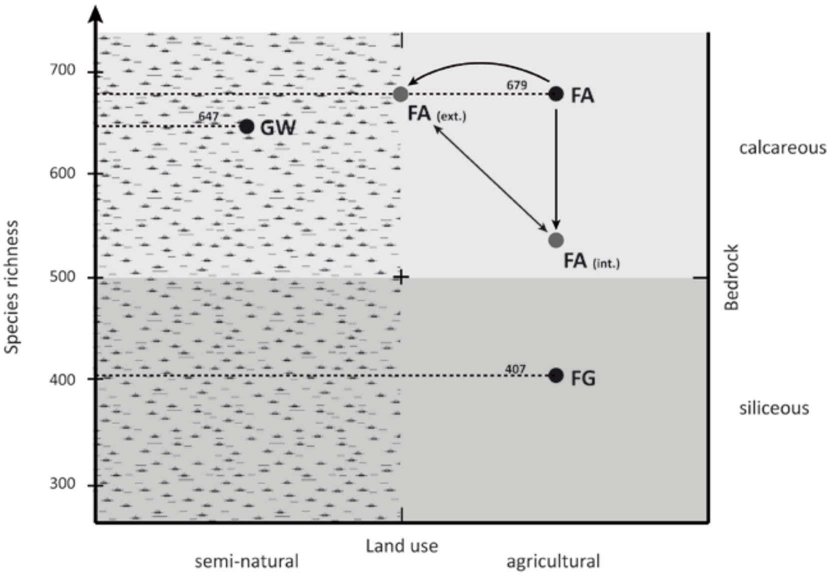


Figure 3-25: Study sites and their species richness. Grafenwöhr (GW) is situated on calcareous bedrock and managed in a semi-natural state. Fichtelgebirge (FG) is situated on siliceous bedrock and intensively farmed. Frankenalb (FA) is situated on calcareous bedrock and extensively farmed (FA_{ext}). Figure shows scenario, if Frankenalb would be intensively farmed (FA_{int}) like Fichtelgebirge and how much bedrock would probably buffer decrease of species.

The figure shows the four possible scenarios. (I) Calcareous bedrock and semi-natural land use. (II) Siliceous bedrock and semi-natural and use. (III) Calcareous bedrock and agricultural land use. (IV) Siliceous bedrock and agricultural land use. Grafenwöhr (GW) is clearly part of (I), Fichtelgebirge part of (IV). Frankenalb (FA) was expected to contain the combination of calcareous bedrock and agricultural landscape (III). However, results show, that land use is less intensive (extensive = ext.) than at Fichtelgebirge and therefore has to be placed between the two land-use types (FA_{ext}). FA_{int} shows the hypothesized reduced species number of Frankenalb if it would be under similar intensive agricultural land use like Fichtelgebirge.

Re-analyzing the regressions between species richness and the number of land-use types per plot, the number of disturbance types per plot and the number of patches per plot, respectively, shows that the graphs actually contain two parts. The first part is where both Frankenalb and Fichtelgebirge show the same number of variables on the x-axis. The second part shows the heterogeneity of Frankenalb and Grafenwöhr. With a similar number of disturbance types and a similar number of patches in a plot, Frankenalb has a higher species richness than Fichtelgebirge (Figure 3-26). This difference between the species numbers proves the influence of bedrock and supports our first hypothesis.

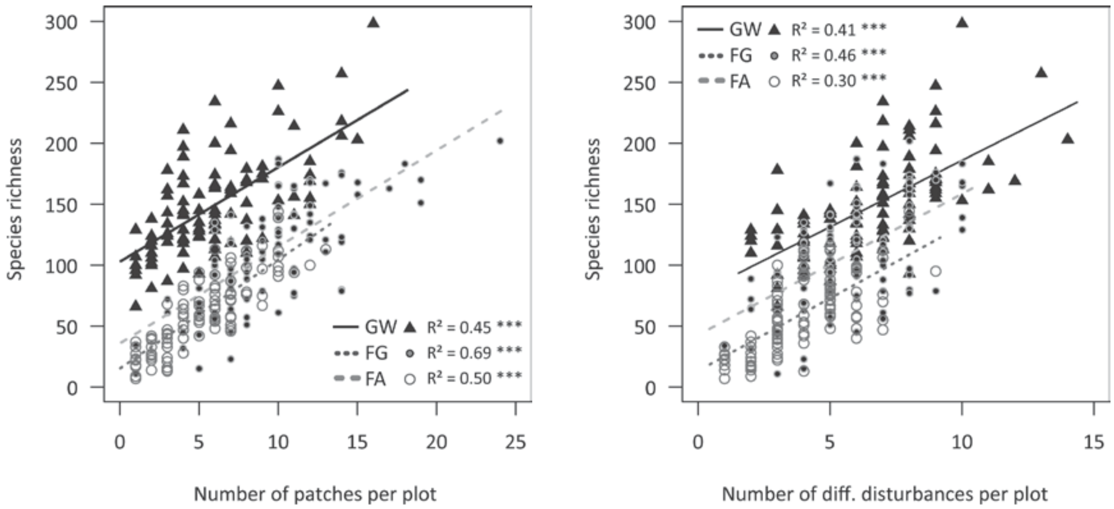


Figure 3-26: Linear regressions between species richness and number of patches per plot (left) and species richness and number of different disturbances per plot (right). With a similar number of disturbance types and a similar number of patches in a plot, Frankenalb has a higher species richness than Fichtelgebirge, which might due to the bedrock effect.

However, this intensity of agricultural land use predominantly occurs in the open landscape. Analyses showed a highly significant influence of forests on species richness at the semi-natural landscape only (mean: 84.7 plant species per patch). At the agricultural landscape (FG - mean: 18.5; FA - mean: 25.7) forests were very species poor. Therefore a splitting of the data sets was necessary. Analyses showed a similar picture like in the open landscape plots. Both, the semi-natural landscape and Frankenalb as agricultural landscape show the most significant influence due to the heterogeneity of the disturbance regime, too. Analyses with the most intensely used Fichtelgebirge were not successful (model breakdown). However, in combination with the two other data sets the forests of Fichtelgebirge are rather influenced by the selectivity of the tree felling.

H5) Disturbance regime is more important than abiotic heterogeneity and patch size in agricultural landscapes due to the homogenizing effect of agriculture at patch scale

This hypothesis clearly has to be denied. In all three data sets, the abiotic factors play a more important role on patch scale than the disturbance regime. The different multivariate analyses showed a regularity concerning some indicator values. The variances of the Ellenberg indicator values seemed to be especially relevant. These variances show the amplitude between the maximum and minimum indicator value and therefore are an indicator of heterogeneity of a landscape. The bigger the variance was the more niches were expected that enhance species richness. However, since these niches occur all over a landscape, a more detailed look at the analyses needs to be taken.

In open landscape patches, the minimum value of nitrogen (Nmin) always had a negative influence on species richness. Nitrogen is the limiting nutrient for plant richness and composition (Vitousek & Howarth 1991; Clark & Tilman 2008). Highest species richness is found on meadows with intermediate nitrogen supply (Jacquemyn *et al.* 2003; Zechmeister *et al.* 2003; Roth *et al.* 2013). According to Wilson & Tilman (2002), additional nitrogen significantly decreases the colonization process. However, at our study sites, pure eutrophic areas did not exist.

At Fichtelgebirge, the maximum values of humidity (F) and pH (R) showed a significant positive influence. A possible explanation for the combination of high humidity and a high pH might be the location of the meadows in a valley where, due to the acidic bedrock, liming is conducted to increase the soil pH. These valley bottoms usually are more humid than higher elevated areas. Since the study site of Fichtelgebirge had several water bodies, the direct neighborhood of a meadow to a water body could enable this combination. In fact, several locations could be distinguished where this happened. At two locations, the combination of a high humidity and a high pH value occurred in settlements (high humidity due to sealing) and adjacent meadows. Not significant were the occurrence of minimum pH (R.min) and nitrogen (N.min) predominantly on paths / roads and maximum nitrogen (N.max) on grassland and transition zones, which usually are fertilized.

At Frankenalb both the maximum and minimum values of pH (R.min, R.max) were significant. Since Frankenalb is situated on basic bedrock, the interesting contrast is given by the minimum values. Most of them were found on paths or roads but also in transition zones. These transition zones were predominantly road verges. The significance of light availability, which was not found at Fichtelgebirge, can be explained with a high bush encroachment in the open and not that intensively used landscape of Frankenalb.

At the semi-natural landscape of Grafenwöhr, most significant abiotic parameters were maximum and minimum values of pH (R.min, R.max) and humidity (F.min, F.max) and furthermore, the maximum values of nitrogen (N.max) and the patch size (area). The minimum pH-values could not clearly be distinguished but they mostly occur in transition zones and fallow land. These zones quite frequently are used for hiding training and most of them are gravelled. The main gravel type is limestone, which can be clearly seen in the results (high pH, low nitrogen; disturbance: compaction by wheels and tracks). However, several paths and small gravel plains have been covered by basaltic material, which shows a very different pH value. Furthermore, gravelled paths usually are dryer than the surrounding, because of the missing water capacity. Regarding the high nitrogen input, the question arose, where this may come from, if there is no fertilization at all. Data showed that predominantly transit zones and grassland hosted the certain plant species. These zones are habitat for hundreds of deer, in my analyses named as macroherbivores. Their impact should not be underestimated in case of both grazing impacts and N input (Frank & Groffman 1998; Rexroad *et al.* 2007; Schrama *et al.* 2013).

Only the semi-natural landscape showed an area-effect. In all three study sites we found large patches. At Grafenwöhr and Fichtelgebirge, some reached a full hectare of size (one-patch plot) in the open landscape. The mean patch size in the open landscape was nearly identical of 1400 m² at Grafenwöhr and 1450 m² at Fichtelgebirge. According to the species-area relationship large areas enclose a higher species number than small areas (MacArthur & Wilson 1967). Consequently, the two study sites should have contained a similar number of species. However, our results showed a triplication of species numbers at the semi-natural site. At the semi-natural landscape these large patches were mostly grassland, at Fichtelgebirge they were predominantly fields. As indicated in the introduction of this chapter, we find a homogenization and simplification in agricultural fields which extremely reduce species numbers. Boundaries between fields can be very species rich (e.g., Wiens *et al.* 1985; Le Cœur *et al.* 2002; Ma *et al.* 2002) and often usually contain species from the adjacent patches (Tsipe *et al.* 2008). However, these transition zones usually are of linear shape. According to Forman (1981, in Ma *et al.* 2002) linear patches contain reduced species numbers than round shaped patches due to the edge effect. Smart *et al.* (2002) discovered that with increasing productivity on fields the species richness of the boundary reduced in a slower manner than in the field itself. Since the similarity decreased in the same time they concluded that boundaries function as refugia. In our study, in the agricultural landscape the average boundary patch contained more species than the fields, nearly similar numbers like grassland, but less species than fallow land.

At Frankenalb the maximum size was approximately 8600 m². This is close to the maximum size of the two other sites. The biggest patches were either fields or meadows. However, the mean patch size was only 693 m². In hypothesis four we discovered the effect of the differing land-use intensities between the two agricultural landscapes. Frankenalb showed a small scaled heterogeneity with less intense impact. At least on regional scale the landscape heterogeneity supports species richness more than the size of a patch (Austin 1999; Kreft & Jetz 2007) because of the higher number of different niches (Rosenzweig 1995; Crawley & Harral 2001). However, at Frankenalb mean species richness on patch size was not much higher than at Fichtelgebirge, but the overall species richness supports this hypothesis.

At this stage, a summary of the results of Grafenwöhr seems to be necessary. We find as big sized patches and rather low patch numbers as at Fichtelgebirge and therefore a less heterogeneous landscape than at Frankenalb. Still, we find an as high gamma diversity as at Frankenalb. In hypothesis one, we found evidence for the bedrock effect. In hypothesis two and three, the natural disturbances and the heterogeneity of the disturbance regime were added as main driver for species richness. However, the lower heterogeneity at Grafenwöhr leads to a reduced number of niches and therefore to objections to the niche-based approach. Hence, stochastic factors might play an additional role. Here we come to the neutral theory of Hubbell (2001). This theory considers the possibility for speciation or dispersal of individuals (Alonso *et al.* 2006). Due to the mixture of patches of all sizes and the corridors within the semi-natural landscape these processes might play an important role.

In the agricultural landscape the area effect was not relevant because of homogenization. It was expected that this would influence abiotic factors due to agricultural land use. However, we still found evidence for the abiotic heterogeneity. Therefore we can conclude that there must be a further explanation for species richness and distribution. Here as well, seed dispersal might be one possible explanation. Species trait analyses show a selection towards well dispersed species in the agricultural landscape in comparison to the semi-natural landscape (Buhk *et al.* 2014). Especially anthropogenic disturbances and a simplification and increasing similarity between habitats in a landcape are some of the main drivers for biotic homogenization (Olden & Poff 2003; Olden *et al.* 2004; Lambdon *et al.* 2008). Furthermore, this homogenization process is related to changes in the natural colonization and extinction rates (Olden & Poff 2003; Florencio *et al.* 2013). Agricultural land use may act as filter for light weighted and long-distance distributable species. Approximate maximum distance for wind-dispersed seeds was 500 m (Thomson *et al.* 2011; Auffret 2013), the majority of diaspores fly less than 100 m (Nathan *et al.* 2002; Tackenberg 2003; Soons *et al.* 2004). Because of the large patch sizes of fields (and meadows) in agricultural landscapes, it is highly likely that seeds transported by wind alight on soil or vegetation (Bullock & Moy 2004; Benvenuti 2007). According to Zanin *et al.* (1997), plants distributed by anemochory (wind-dispersal) are typically the first to establish in untilled agrosystems. Since we found evidence of abiotic heterogeneity, mainly in the semi-natural habitats of the agricultural landscape, we assume that biotic homogenization plays a crucial role for species richness and composition. However, the question is if speciation of individuals occurs, as suggested by the neutral theory, or if the opposite takes place that this biotic homogenization effect reduces specialists and promotes generalists (Wilson *et al.* 2009; Auffret 2013).

H6) The common hypotheses IDH and HDH are valid

Results show that the heterogeneity of the landscape plays a significant role for species richness on landscape scale. It therefore supports the 'Habitat Heterogeneity Hypothesis' (MacArthur & MacArthur 1961) and 'Mosaic Concept' (Duelli 1997). Several studies found similar results (e.g., Zechmeister & Moser 2001; Deutschewitz *et al.* 2003; Waldhardt *et al.* 2003; Jentsch *et al.* 2012). The heterogeneity of the disturbance regime significantly increased species richness on landscape and on local scale. This effect was found in both the agricultural and especially in the semi-natural landscape. Best indicators for heterogeneity were the introduced fuzzy variables. The term 'number of different…' already assumes a combination of different parameters at the same location. These fuzzy variables were most significant on plot level. Therefore, this hypothesis is validated on landscape scale. At patch scale, abiotic variables played a more important role than the disturbances. However, here particularly the variances of Ellenberg indicator values showed the most significant influence. These variances cover the range between the minimum and maximum value. Thus, a wide range (i.e. high value of variance) indicates a variety of abiotic niches within a patch and therefore a high heterogeneity.

A validation of the 'Intermediate Disturbance Hypothesis' (Grime 1973; Connell 1978) is not that easy. The multivariate regression analyses did not show any significance regarding the parameters related to IDH. Further regressions between patch size, species richness and the quantitative IDH (see methods) showed a week positive effect of IDH at Grafenwöhr, no effect at Frankenalb and a negative effect at Fichtelgebirge. The conclusion is that the IDH has to be denied, at least in the manner how I decided, what an intermediate level is.

One of the major concerns about the IDH is the way, how to properly define the hypothesis (see current debate Fox 2013 a, b; Sheil & Burslem 2013). Besides the theoretical uncertainties, empirical studies often fail to find a hump-back shaped species peak at intermediate level. There are as many studies confirming the hypothesis as studies denying it. One reason could be that researchers "failed to sample a sufficient range of disturbance frequencies or intensities" (Fox 2013b). Or in different words, they missed to distinguish the intermediate level of the organism they were looking at. This is a crucial point. The IDH needs to be seen in a nuanced light, since a disturbance has different spatial and temporal characteristics. We find variances in frequency (time), size (space) and intensity (impact), but also the time after the disturbance and therefore the starting point for resilience. Depending on the organism the ranges of these variances may significantly vary. A first uncertainty is if we consider a community of species or just a single individual. As an example, the range of variance in impact size to a plant community (decimeters to meters) would be different than to a single plant species (millimeters to centimeters). A second uncertainty is the life span of an organism. An intermediate frequency of disturbance that hits a tree cannot be compared with the one that affects a perennial herb. One way would be to specifically observe a certain species (community). Hobbs & Huenneke (1992) suggest relating the frequency of discrete events to the longevity of major species. However, this is only possible in experiments and needs an exclusion of all other not relevant species. In nature, processes superimpose and species interact. Apart from catastrophic events that set back a whole system, a disturbance creates niches on a certain spatial level. Therefore, some species would be affected if they belong to this certain scale, for the others there would not be any effect at all. The ideal and theoretical approach is the co-existence as mixed community at an intermediate level which leads to a climax of species numbers (see figure 1.5.4 – IDH hump-back). However, this climax is dynamic and difficult to distinguish. Graham & Duda (2011) add their concern about the high heterogeneity an intermediate disturbance creates. This is only possible when the original environment is homogeneous. In already heterogeneous environments the effect would be much less.

My classification of intermediate level was straight forward. Out of the different disturbance descriptors the intermediate classes of 'frequency', 'size' and 'duration', indicating the intensity of a disturbance, were used. For 'frequency' these were the categories once a year, twice a year and three times a year. Now the impact depends on the disturbance type. In a mowing regime, this selected intermediate level actually shows nearly the full variance of regular mowing. A higher frequency we would find in some boundaries, gardens or golf ranges. A mowing frequency of once a decade would lead to succession and bush encroachment. My intermediate categories for 'duration' were less than one week and less than one month of disturbance impact. Since most of the regular disturbances last less than one day, these categories are rather assigned to material storage, flood or dehydration events, pond drainage and pesticide application. My intermediate categories of 'size' were 50-75% of affected patch size. These are related mostly to mowing, fertilization and consequently the driving with tractors.

Since I did not distinguish between organisms or communities but did the same analysis for the whole system, two questions arise. How to judge my results? What would I expect from the groups where my classification did not meet the right variation?

At the semi-natural landscape there was a positive correlation between patch size, species richness and quantitative IDH. In principle one can state that the bigger the size of a patch is, the higher is the probability that one or more disturbances belong to the intermediate level. However, even at the smallest patch sizes some multi-intermediate disturbances were recorded. One effect could be the overlapping natural and anthropogenic disturbances. A higher number of disturbance types in one patch increases the number of intermediate disturbances. At Frankenalb there was no area effect on a higher abundance of intermediate-related disturbances. Patch sizes are smaller at Frankenalb, which might be the reason for this result. In comparison with the semi-natural landscape, the number of different disturbance types and the average disturbance number were as low as at Fichtelgebirge. However, the more extensive land-use left a neutral result for intermediate levels.

At Fichtelgebirge an increasing area led to a decrease in the intermediate disturbance level. The biggest patches were mostly fields. Frequencies are usually higher with crop rotation, fertilization and tillage. The size of these disturbances exceeds the intermediate range which I selected. Farmers try to get the maximum out of their fields. Consequently, they would work on the full extent of the patch or plot. Therefore is has to be stated that the disturbance classification key is not completely suitable for the analysis of the IDH, because especially in the categories size and duration the classification would need a better and party higher resolution.

Beta diversity

The agricultural landscapes showed nearly similar species numbers on patch scale, whereas they differed much on landscape scale. In agricultural lands, we often find abrupt differences in species composition from one patch to the adjacent one, especially if they belong to different land owners. Therefore I assumed that inter-plot similarity in the two agricultural landscapes is low. Clough *et al.* (2007) compared arthropods on organic and conventional farms. They discovered that management did not have an effect on α-diversity. However, β-diversity was higher on conventional fields and enhancing overall species numbers. In contrast, Karp *et al.* (2012) reported a declining β-diversity with land-use intensification. In my case, both landscapes are conventionally managed, but differ in intensity and bedrock, whereas the latter mainly causes the higher species richness at Frankenalb. Fichtelgebirge showed the lowest mean inter-plot similarity, however with higher variability than the Frankenalb data. In comparison, the semi-natural landscape, which was expected to have a high similarity of neighboring plots, because of missing constraints, did show a higher but not that significant mean and maximum similarity. A low similarity despite the high total species richness must therefore have a further reason. Rare species do not really enhance similarity, because it is very likely that they do not occur on the other plots due to their rareness (Morlon *et al.* 2008). Since both Grafenwöhr and Frankenalb had many rare species (see chapter 4), this might be an answer.

Community similarity decreases with geographic distance. Soininen *et al.* (2007) related three processes to this decay of similarity. First, a change in environmental conditions enables new niches for different plant species (Tuomisto 2003). Second, barriers hinder dispersal (Garcillán & Ezcurra 2003; Keller *et al.* 2012). Third, ecological drift and random processes lead to a general decay (neutral theory - Hubbell 2001).

Distance decay was shown at the semi-natural landscape but barely presented in the agricultural landscapes, although the extensive agricultural site showed a weak decay. One reason can be the dispersal ability of plants selected by agricultural land-use (effective long distance dispersers) which leads to a lower distance decay. Another reason, which is still under debate, is the scale of observation (Nekola & McGill 2014).

Chapter 4

4 MERITS & THREATS – DISTURBANCES AND THEIR IMPLICATIONS FOR NATURE CONSERVATION

4.1 INTRODUCTION

In chapter two and three I focused on plant species richness and the relation between biodiversity, land use and disturbances. In this chapter I will put my focus on the quality of species and their value for nature conservational issues. The value of a habitat for nature conservation depends rather on the amount of rare species than on total species richness (Alatalo 1981; Gaston 1994). Species are characterized as rare, when they display a low frequency or abundance within an area (Gaston 1994). Threatened and endangered species, however, are based on estimations of the probability of a taxon to extinct and are classified in different categories and listed in national and international registers (e. g. IUCN 2012; LfU 2002).

What defines a species and its value to justify the need for protection? The Federal Law on Nature Conservation (BNatSchG 2009 §54, Abs. 1 & 2) defines them as a) species that are endangered because of human impact within Germany, and b) species that are endangered worldwide and for which the Federal Republic of Germany has the responsibility to protect them. The Federal Agency for Nature Conservation (BfN) (http://www.bfn.de/0322_pflanzen.html) gives the following reasons and order for the reduction of species:

1) Habitat destruction (settlements, roads, mining)
2) Agricultural land use: either abandonment or intensification of traditional extensive agricultural land use on pastures and fields
3) Forestry: afforestation of open habitats, building of forest roads, drainage, monocultures of alien forest species, especially conifers, reduction of natural thinning, removal of old trees and deadwood
4) The hunting system with a too high density of game
5) Habitat changes with additional nutrient input that endangers pioneer species

This list of reasons underlines that the topic of nature conservation bears a high potential for conflicts between stakeholders, because in general it requires a reduction of anthropogenic impacts which often affect economic interests. However, rare and endangered species are found also in agricultural landscapes. Before the start of agriculture 7500 years ago, Central Europe consisted of tundra and forests, with fragments of alluvial and alpine grasslands (Ellenberg & Leuschner 2010; Hejcman *et al*. 2013). Due to the historic transformation into a cultural and therefore open landscape, niches allowed habitat for a variety of plant species that spread into Central Europe from other regions like the steppe regions in the east or the Mediterranean in the south (Poschlod & WallisDeVries 2002; Pärtel *et al*. 2007). Semi-natural grasslands and calcareous grasslands are among the most species-rich habitats and are refuge for several rare and endangered species (Eriksson *et al.* 2002; Poschlod & WallisDeVries 2002; Duelli & Obrist 2003). However, because of land-use changes (especially intensification and abandonment), these habitats have significantly declined (models predict a reduction of 50% until 2080 - Rounsevell *et al.* 2005) and several of those species disappeared again (Eriksson 2012). The Red List of Sweden, for example, lists 68% of their endangered plant species occurring in agricultural landscapes (Gärdenfors 2010 in Eriksson 2012).

The aim of nature conservation efforts, like the agri-environmental schemes (European Commission 2009) is, to protect theses rare species. However, they compete with economic interests and conventional farming practices (Knop *et al.* 2006; Buhk *et al.* 2007b; Kleijn *et al.* 2009) and their outcome is judged ambivalently (Henle *et al.* 2008; Pe'er *et al.* 2014).

In contrast to the view on agricultural landscapes, military training areas are considered as very species rich. Several studies prove that threatened and endangered species are especially found on military land (e.g. IUCN 1996; Gazenbeek 2006; Naturstiftung David 2007; Warren *et al.* 2007; Warren & Büttner 2014). Consequently, conservation is conducted to maintain a high ecological status quo.

The fact that historic agriculture lead to the spread of the rare species of today contradicts with the mentioned aspect that agriculture is one of the major threats to endangered species (Helsen *et al.* 2011). We need to consider more detailed, what parameters support or impede rare species. Luoto (2000) found a maximum of rare plant species in heterogeneous environments, and Warren & Büttner (2006, 2014) accordingly state that several endangered species are dependent on disturbances. Luoto (2000) sees an intermediate disturbance level as driver. Furthermore, a recent study describes narrow abiotic soil conditions as explanation for the occurrence of rare species (Wamelink *et al.* 2014).

Land-use change implies different levels in a) disturbance intensity and b) resource availability (Lindborg & Eriksson 2004a). Disturbance intensity (a) is characterized by the frequency, duration and spatial extent. MacArthur & Wilson (1967) introduced two fundamental types of reproductive strategies, r- and K-strategists. Ruderal (r-) strategists are found on disturbed ground where competition is reduced, whereas K-strategists need constant conditions over a longer time period. Plants range in the spectrum between the two antagonistic extremes.

Depending on the organism, a disturbance can be without any consequences or fatal (Pimm 2001; Tuomainen & Candolin 2011). Orth & Warren (2006) therefore differentiate between disturbance-dependent, disturbance-tolerant and disturbance-averse species.

Resource availability (b) depends on the land use and environmental factors. As example, intensive agricultural land use bears the risk of an oversupply of nutrients and eutrophication, whereas extensive or abandoned land use especially in oligotrophic habitats leads to deficiency. Drainage can lead to changed environmental conditions and, like the removal of vegetation cover, to dry conditions. A plant species that cannot cope with this stress would start to show damage symptoms.

According to Hutchinson (1957), each species has its own n-dimensional ecological space, an ecological niche, with abiotic conditions in a certain range. Since plants compete for light, water and nutrients, they need to form characteristics and strategies to secure survival (Craine *et al*. 2013). If nutrients are sufficiently available, either naturally or artificially, there is a significant competition between high-competitive species. With limited resources (e.g., nutrients, light and water) or unfavorable environmental conditions (e.g., extreme temperature or pH), stress is caused. Under stress conditions, species with low competitive abilities, like red-listed species (Schön 1998), find their habitat.

Grime extended the two strategy types of MacArthur & Wilson (1967) by the strategy of stress tolerance (Grime 1974, 1977 - see CSR in the box). In applying the theory, a plant community can be characterized in terms environmental conditions and management factors and can therefore be used for conservation and management recommendations (Hunt *et al.* 1991; Wilson & Lee 2000).

IN THE BOX: Grime's CSR-strategy types

C-strategy (competitors):	long-living and high-competitive species with ideal conditions, low disturbance, low stress about resources
S-strategy (stress tolerators):	extreme site conditions, resources difficult to reach, long-living with slow reproduction; low disturbance, high stress
R-strategy (ruderals):	short-living, fast reproduction; high disturbance, low stress

Furthermore transition types CR, CS, SR, CSR

Plants develop traits which they use for their strategies to save resources. These are mainly related to dispersal, like reproduction, seed number and dispersal strategy. In combining them with Grime's CSR-types, one gets comprehensive information about a location.

IN THE BOX: Functional traits & CSR

C-strategy (competitors):	fast growing (lateral, vertical, root mass), clonal reproduction[1], development of rhizomes and stolons, long-living (perennials). (e.g., McIntyre et al. 1995; Kleyer 1999; Schippers et al. 2001; Cofrancesco et al. 2007; Kowarik 2010; Eilts et al. 2011)
S-strategy (stress tolerators):	slow growth rate, possibility of nutrient retention (e.g., Grime 1979)
R-strategy (ruderals):	short life spans (annuals), high seed production (high intrinsic growth rate), low seed weight[2], meteochory for dispersal. (e.g., MacArthur & Wilson 1967; Grime 1979; Fahrig 1991; McIntyre et al. 1995; Barik et al. 1996; Klotz et al. 2002; Kotanen 2004; Lososová et al. 2006; James 2008; Gomez-Garcia et al. 2009; Altermatt et al. 2011; Merou et al. 2013)

[1] Other studies found more clonal reproduction under highest disturbance intensity (Fahrig et al. 1994; Gomez-Garcia et al. 2009); [2] Another study found higher seed weight under high disturbance Rusterholz et al. 2009

Generalist species show a larger tolerance for environmental conditions and therefore are wider distributed, whereas specialist species are bound to narrower environmental conditions. Warren *et al.* (2001) stated that habitat specialists would be more affected by habitat loss and habitat degradation than generalist species. With increasing disturbance intensity generalist plant species dominate (Devictor *et al.* 2008; Chiron *et al.* 2010; Clavel *et al.* 2011).

However, besides the valuable species that are worthy to protect, disturbances promote several undesirable species (Mack *et al.* 2000; Deutschewitz *et al.* 2003; McKinney & La Sorte 2007; Uddin *et al.* 2013; Jauni *et al.* 2014), like non-native species.

The natural process of expanding areal of flora and fauna is exceeded many times over by the accidental or deliberate introduction of non-natives due to human activity (Nentwig 2008; Kowarik 2010). Mack & Currie (2000) call it the second severe impact on biodiversity after habitat loss. In our study areas, we expect gateways for alien species in agriculture, for example in form of uncleaned seed mixtures (Hougen *et al.* 2012), in settlements due to ornamental plants in gardens (Dehnen-Schmutz *et al.* 2007; Niinemets & Peñuelas 2008) and on the military training area because of international troop transports and contaminated vehicles (Westbrook & Ramos 2005; Cofrancesco *et al.* 2007; Nentwig 2008; Weldy 2008). Within the areas, these species are distributed along roads or train tracks and rivers (Fosberg 1959; Schmidt 1989; Tyser & Worley 1992; Lippe & Kowarik 2007; Pollnac *et al*. 2012), or by vectors like wind (anemochory) or animals (zoochory) (Vellend *et al*. 2004). Most non-native species are generalists (Büchi & Vuilleumier 2014), can establish in disturbed grounds and benefit from their abilities of long-distance dispersal (Wilson 1988; Hill *et al.* 2002). This might be a key reason for their success in disturbed areas (Catford *et al.* 2012). Introduced species bear two risks: the reduction of the native flora and its biotic and functional homogenization homogenization (Elton 1958; Eriksson *et al*. 2002; Winter *et al.* 2008; Clavel *et al.* 2011; Douda *et al.* 2013). Olden *et al.* (2004) identified three classes of homogenization. These are (i) taxonomic homogenization, (ii) genetic homogenization and (iii) functional homogenization. Winter *et al*. (2008, 2009) extended the list with the phylogenetic homogenization. In my study I will survey if increasing disturbance influences and changes certain functional traits towards the characteristics of generalists.

All these factors are important for nature conservation issues. Therefore we group our hypotheses in three categories.

a) Red-listed species

H1) The military training area contains more rare species than the agricultural landscape

H2) The occurrence of rare species is linked to disturbance intensity, abiotic conditions and land-use type

b) Alien species

H3) Military training increases the number of alien plant species. They are distributed all over the area whereas in agricultural landscapes we find alien species along roads and on road margins.

c) Biotic homogenization

H4) High disturbance supports generalists, such as alien species. They are characterized by high seed weight and seed production (=high distribution capacity), short life-cycle (annuals) and wind dispersal.

4.2 STATISTICAL METHODS

All data were splitted in open landscape and forest data. Regressions and box-whisker-plots were calculated using the open source software R version 2.15.3 (R Core Team 2013).

Information about red list status was derived from the Bavarian Red List (LfU 2002) and the online data base (www.floraweb.de). The following categories were recorded on our three study sites:

- RL-1: critically endangered (CR)
- RL-2: endangered (EN)
- RL-3: vulnerable (VU)
- RL-G: endangerment is expected
- RL-V: near threatened (NT): not endangered yet, but several factors may lead to endangerment within the next 10 years)

The categories RL-G and RL-V were combined.

Plant life history characteristics were derived from Biolflor (Klotz *et al.* 2002) and LEDA (Kleyer *et al.* 2008) databases.

- Preproduction type (vegetative / seed) - Biolflor
- Dispersal strategy (anemochory, zoochory, autochory) - LEDA
- Ecological strategy - CSR (Grime 1974; 1979) - Biolflor
- Seed number - LEDA
- Seed weight - LEDA
- Number of biotopes (specialists/ generalists) - Biolflor
- Life cycle - annuals / perennials – Biolflor

For analyses, CSR strategy types were reclassified according Burmeier *et al*. (2010). They allocated in sum three points to the possible combinations with C, S, and R strategies. As example, a pure C-strategist would receive three points, whereas all other strategies (R, S and combinations) were allocated 0. A CR-strategist would receive 1.5 points for C and 1.5 points for R. A CSR-strategist would receive 1 point each strategy. The same system was applied for seed reproduction (clonal, seed, both). A modified system with four categories (0, 1, 1.33, 2, 2.66, 4) was applied for dispersal strategy types (anemochory, hemerochory, zoochory, autochory).

Disturbance intensity was classified using the disturbance characteristics ‘frequency’, ‘duration’ and ‘size’ as parameters. Three classes were created.

(1) Low disturbance:

- Frequency: 1x/century; 1x/decade; none
- Duration: <1 day; none
- Size: ¼ area; linear/punctual; none

(2) Intermediate disturbance:

- Frequency: 1x/year; 2 x/year; 3 x/year
- Duration: <1 month; <1 week
- Size: ½ area, ¾ area

(3) High disturbance:

- Frequency: >3x/year; steady intense; steady diffuse
- Duration: <1 year; >1 year
- Size: 4/4 area

Principle Component Analyses (PCA) were conducted to analyze the influence of abiotic parameters on species richness and the occurrence of threatened and endangered species.

Ellenberg indicator values not only show different variances in our landscapes (e.g. light (L): 1-9, salinity (S) 0-2) but also different minimum and maximum values. Since PCA analyses weight high values different than low values, results were falsified. Therefore the values were transformed as followed: $\text{Ellenberg}_{\text{single-trans}} = \text{Ellenberg}_{\text{single-original}} - \text{Ellenberg}_{\text{all-mean}}$

This led to an untouched variance but adjusted maximum values. For explanation of patterns in species richness and the occurrence and distribution of threatened and endangered species, the values L, F, R and N were used. Analyses were conducted using unweighted values. Significance was determined by uncertainty test with full cross-validated.

Multivariate analyses were conducted applying Partial Least Squares Regressions (PLS-R). The method is explained in detail in chapter 2.3. Analyses were conducted using similar data as in chapter three. However, the dependent variable ‘species richness’ was exchanged by the variable ‘red-listed species’. For Partial Least Squares Regressions (PLS-R) and Principle Component Analyses (PCA), the software Unscrambler version X 10.1 (CAMO 2010) was used.

Analyses of variance (ANOVA) were conducted to test the significance of the influence of disturbance intensity on several plant functional traits, using the software SPSS 21 (IBM Corp.). In case that data were not normal distributed, ranked data were used for further univariate analyses. Finally, independent sample tests, based on Kruskal-Wallis non-parametric independent tests and pairwise multiple comparisons (Dunn 1964) were conducted.

4.3 RESULTS

H1) Military training area contains more rare species than the agricultural landscape

In the conventional agricultural area of Fichtelgebirge, clearly less red-listed species are found in comparison to the more traditional agricultural landscape of Frankenalb and the military training area of Grafenwöhr, which showed similar number of endangered species. Species with the highest protection status (RL-1 and RL-2) are especially found in Frankenalb (Figure 4-1).

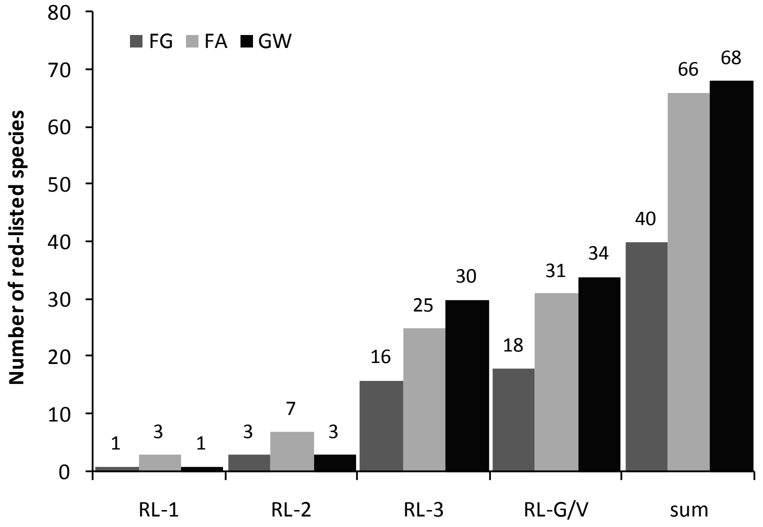


Figure 4-1: Number of red-listed species at Fichtelgebirge (FG), Frankenalb (FA) and Grafenwöhr (GW). Categories are: critically endangered (RL-1), endangered (RL-2), vulnerable (RL-3), threatened/near threatened (RL-G/V).

Numbers of threatened species in relation to total species numbers, however, showed very similar portions (Table 4-1). Major differences in relative numbers of endangered species are found only between open landscape and forest patches. In forests at Grafenwöhr, 19% less threatened and endangered species occur than in the open landscape. At Frankenalb and Fichtelgebirge, however, forests are much poorer in threatened species in relation to species numbers, (30% and 37%, respectively).

Table 4-1: Proportion of red-listed species in total species richness in open landscape and forests in the three study sites. Since there are several shared species, total number is no addition of forests and open landscape. Results show a similar proportion between the study sites in open landscapes and a decay with increasing land-use intensity.

Proportion of RL in SR (%)	**FG**	**FA**	**GW**
Open landscape	10.1	10.6	10.5
Forest	6.3	7.4	8.5
Total	**10.3**	**11.6**	**11.5**

Correlating the number of rare species with the species richness, revealed that the number of threatened and endangered species is closely correlated to the number of species (Figure 4-2).

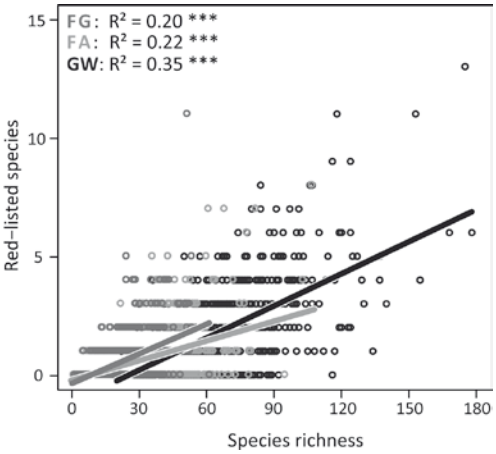


Figure 4-2: Linear regression between species richness and red-listed species shows significant correlation between the number of rare species with increasing total species richness.

However, the absolute number of rare species does not consider their abundance. In recording presence and absence data, a species is considered just once per patch. A frequent or dominant species within one patch has the same weight as a single individual. Still, it is possible to calculate the steadiness in observing all patches within a study site.

Results show a significant higher steadiness of Red List species in the military training area, especially the endangered *Lathyrus nissolia* and of several species from the early warning list. In total, three of four patches showed at least one threatened or endangered species at the military training area; twice as many as in the agricultural landscapes. At Fichtelgebirge, forest showed a bisection of endangered species numbers, whereas at the military training area, the percentage of patches displaying rare species was identical between the landscapes (Figure 4-3).

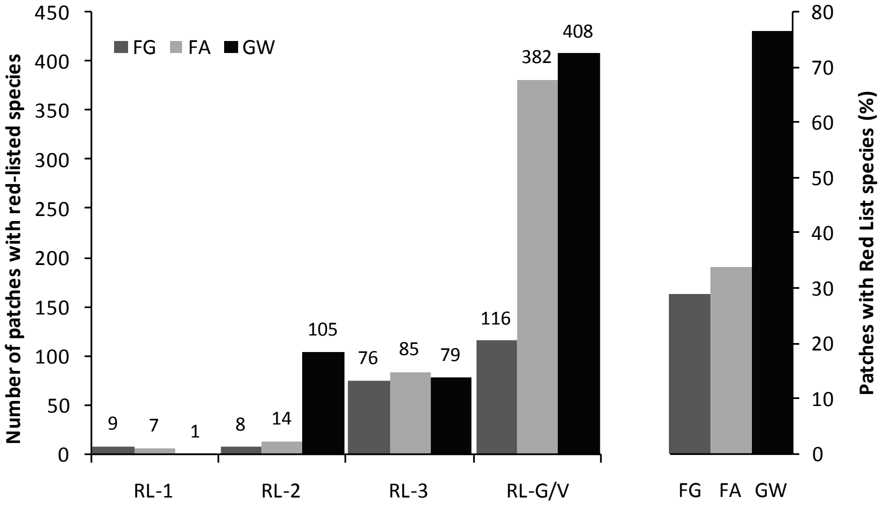


Figure 4-3: Left: Number of patches with the presence of one or more red-listed species, separated by the classification. Right: Percentage of patches with one or more red-listed plant species, separated by study site. Results show that at Grafenwöhr, more the 75% of all patches present red-listed species, more than twice the number as in the agricultural landscapes.

Patches of the open landscape at Grafenwöhr had an average of 2.4 different rare species, which was about 40% more than the two agricultural sites. In forests, the average of 2.9 species was more than double the number of the two other sites (Table 4-2).

Table 4-2: Average number of threatened and endangered species in open landscape and forests of the three study sites.

Average no. red-listed species / patch	FG	FA	GW
Open landscape	1.8	1.7	2.4
Forest	1.4	1.2	2.9

H2) The occurrence of rare species is linked to disturbance intensity, abiotic conditions, land-use type

The observations of the first hypothesis opened new questions about the influence of land use, disturbance regime and abiotic conditions in the study areas and especially the differences between open landscape and forests. To include all parameters and to get an overall picture of the relationships, several multivariate analyses were conducted. Reflecting the results of the analyses of chapter three, conducted with patch species richness (SR), here the analyses were based on the number of different threatened and endangered species (RL) within a patch and were compared with the results of the analyses with total plant species richness of chapter three (all PLS-R figures are displayed in the digital supplement).

Conducting a PLS-R at the **open landscape** at Fichtelgebirge resulted in the highest explanation of the variances of the abiotic parameters humidity (F) and nutrients (N). Negative impact had the low level of nitrogen and the land-use category ‘field’ with agricultural disturbances. These results were conform with the results with species richness as independent variable. Explanation power was 55% (SR) and 33% (RL), respectively.

The analysis with the Frankenalb data resulted in the highest explanation of the variances of the abiotic parameters humidity (F), nutrients (N) and pH (R). Red List species were negatively influenced by low values of N and F. This result is comparable with the analyses in chapter three. Explanation power was 25% for the first axis, compared to 60% in the analyses with SR as independent variable. On the second axis grassland, fallow land and the patch size showed positive and transit zones negative influence on rare species. However, explanation power was only four percent.

At Grafenwöhr training area, the variances of the abiotic parameters N and R and the disturbance regime in grassland (land use, mowing, season) significantly explained the occurrence of Red List plant species. A negative effect had the low values for nutrients and pH. These results were conform with the results in chapter three. Additionally, roads showed a significant negative impact on rare species. Explanatory power was 42% (RL) and 61% (SR) of the first axis.

Analyses of Fichtelgebirge **forest patches** resulted in a poor explanation power of seven percent on the first axis. Humidity and nutrients showed the highest positive influence, whereas thinning had a negative input. The equivalent regression with species richness as variable showed identical significant parameters, though with a much higher validation of 66%.

The analysis of the forests data of Frankenalb resulted in the significance of high light availability and the variances of humidity and nutrients, whereas their minimum values showed a negative influence. The explanation power was 64% (SR) and 21%, respectively. Both analyses showed some influence of the patch size.

The data of the military training area showed similar results with high humidity (maximum and variance) as most significant parameter for both, total species and rare species. A negative correlation were shown by low indicator values on N, R and F. Explanation power was 68% (SR) and 33% (RL). Furthermore, in both analyses the second axis showed some importance of 6% (SR) and 9% (RL), respectively. With RL as independent variable, several variables on the second axis negatively influence rare species, especially the number of different frequencies and disturbances. At the SR analysis, macroherbivory showed positive influence on the second axis.

a) Disturbance intensity

The Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978) suggests maximum species richness with moderate disturbances. Luoto (2000) states that in agricultural landscapes, disturbance regimes with intermediate intensities raise the number of rare and endangered species. To account for these findings, our data were combined and allocated to one of three different levels of disturbance intensity which includes frequency, duration and size of a disturbance. The three levels were i) low disturbance, ii) intermediate disturbance and iii) high disturbance. Results showed that most of the rare species occurred in all three disturbance intensity classes and therefore did not show a preference towards a certain level of disturbance (Figure 4-4). Therefore the hypothesis that the occurrence of rare species is influenced by disturbance intensity was rejected.

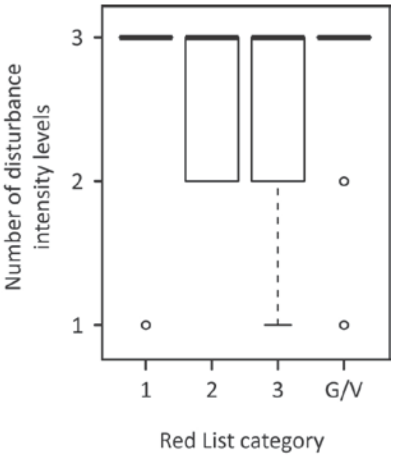
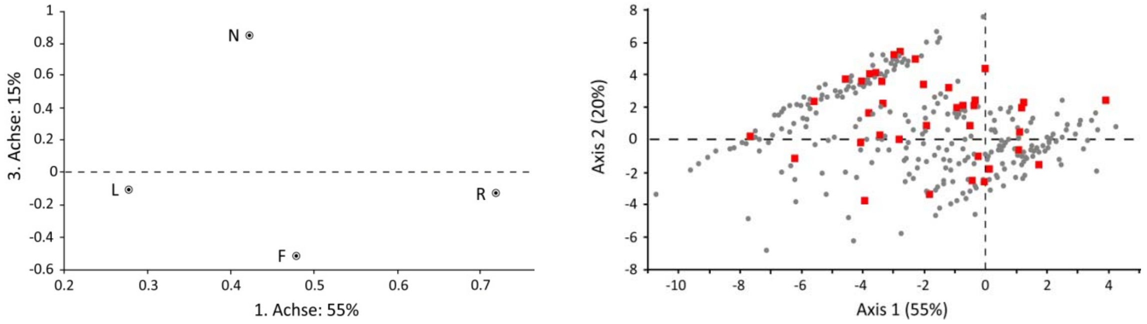


Figure 4-4: Occurrence of red-listed species on different levels of disturbance intensity revealed no preference towoards a certain ditsurbance level.

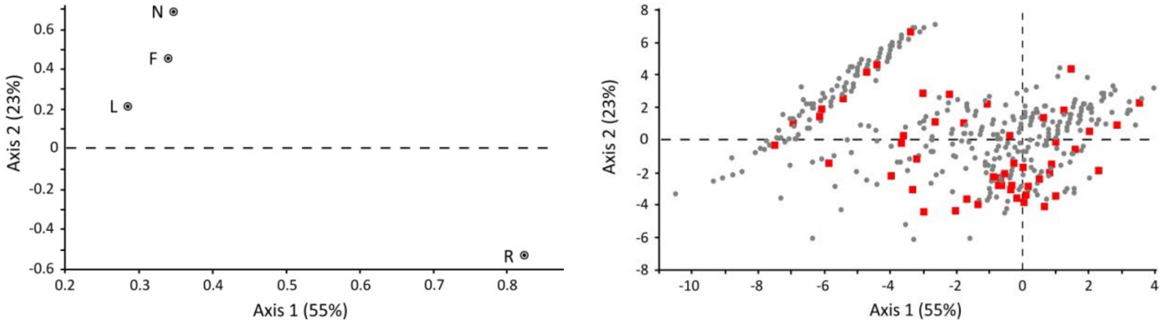
b) Abiotic conditions

For analyzing the influence of abiotic parameters on species richness, several Principle Component Analyses (PCAs) were conducted. The following figures show the results of these analyses for open landscape patches and forest patches in the three study sites (Figure 4-5).

Fichtelgebirge (open landscape)



Frankenalb (open landscape)



Grafenwöhr (open landscape)

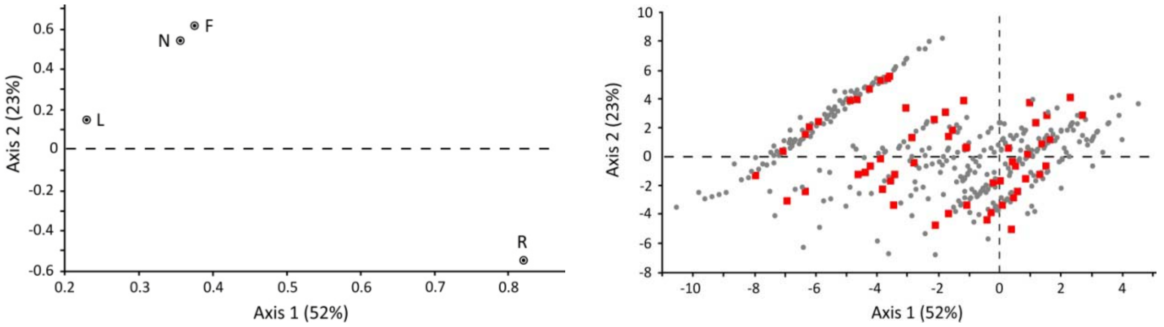
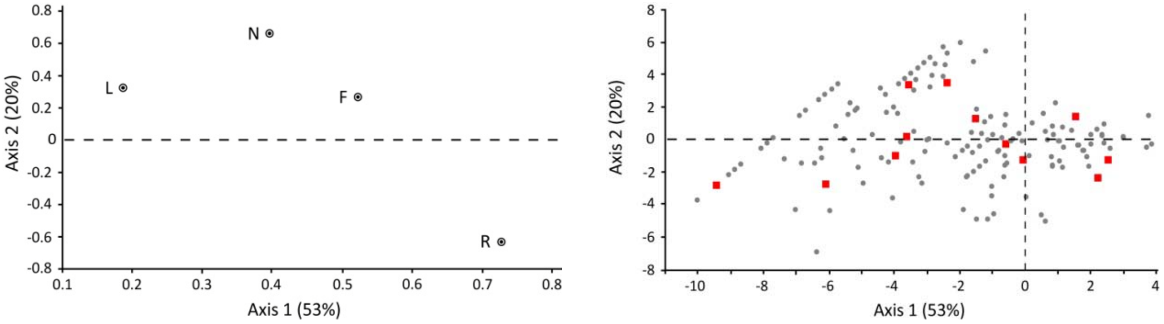


Figure 4-5: Results of the Principal Component Analyses show a very similar distribution and connection of indicator values in all three study sites (figures on left side). Corresponding score distribution (figures on right side) shows plant data points according to their indicator value range. Grey points are common species, red point are red-listed species. Nitrogen shows a negative effect on red-listed species.

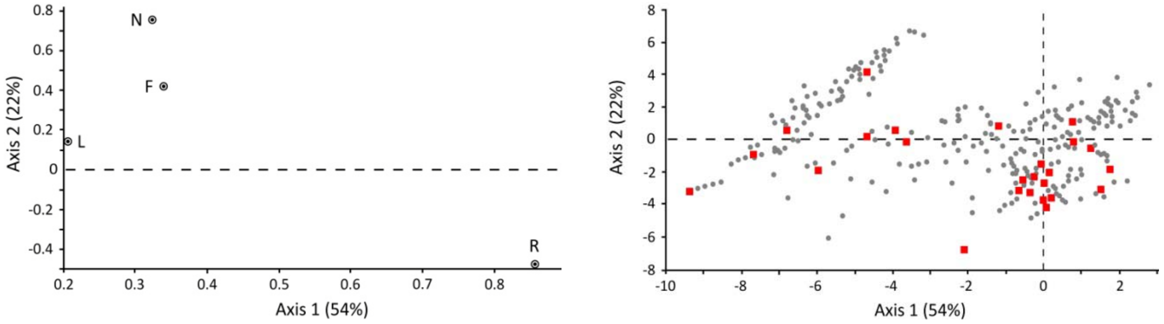
The analyses showed a very similar pattern across the three landscapes, with pH-value as the most important driver for plant species. However, the first and second axis (explanation 52-55%) of the scores-plot show that the occurrence of rare species is not correlated with Ellenberg R-value only, because these species were widely spread. On the first two axes, the three indicator values light (L), nutrients (N) and humidity (F) were correlated. The third axis (explanation 12-15%) clearly separated the high N-level from light and humidity. Here, all three study sites showed no rare species at all in combination with a high N-availability. At Grafenwöhr the indicator values N and F were closely correlated in all analyses.

Identical analyses were conducted for forests in the study sites. Especially at Fichtelgebirge, species numbers were lower compared to the open landscape. Rare species were sparsely and negatively influenced by nitrogen. At Frankenalb, most rare species were correlated with pH. Grafenwöhr and Frankenalb showed a similar connection and distribution of the indicator values (Figure 4-6).

Fichtelgebirge (forest)



Frankenalb (forest)



Grafenwöhr (forest)

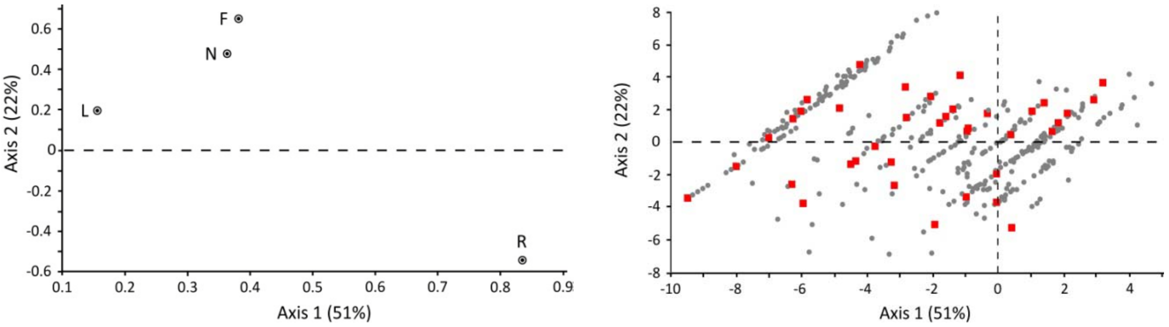


Figure 4-6: Results of the Principal Component Analyses in forests show a very similar distribution and connection of indicator values in all three study sites (figures on left side). Corresponding score distribution (figures on right side) shows plant data points according to their indicator value range. Grey points are common species, red point are red-listed species. Grafenwöhr presented more red-listed species than the agricultural landscapes. High nitrogen values reduce species numbers, especially at Fichtelgebirge.

c) Land-use type

Land use and disturbances are considered as major threat to species richness. For conservational issues, the distribution of endangered species has to be known. Therefore, the occurrence of threatened and endangered species on the different land-use types and their importance as host for endangered species were displayed (Figure 4-7).

At Fichtelgebirge, most threatened and endangered species were found on grasslands, in transition zones and at the banks of water bodies. At Frankenalb, most species were found in transition zones, in forests, on fallow land and on paths. At Grafenwöhr, most rare species were found in forests, on fallow land, in transition zones and on grassland. Despite the results of the PCA that showed no rare species in areas with high nitrogen input, we found some rare species on fields.

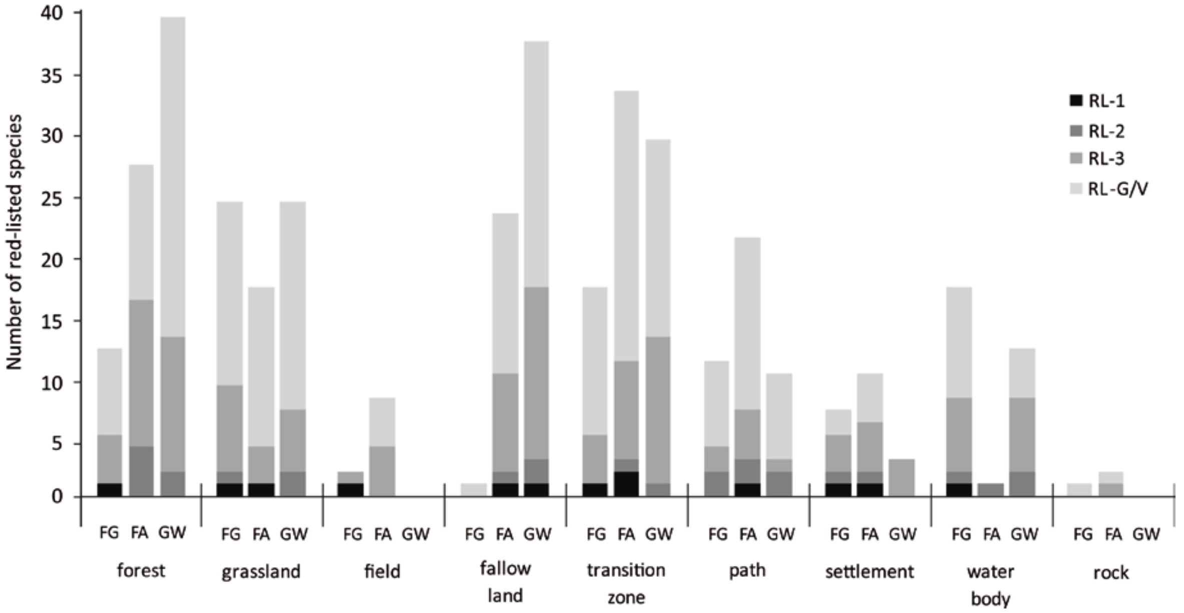


Figure 4-7: Distribution of red-listed species within the different land-use categories. Bar size indicates total number of threatened and endangered species within a land-use type, colors indicate the category. Categories are: critically endangered (RL-1), endangered (RL-2), vulnerable (RL-3), threatened/near threatened (RL-G/V).

A land-use type, that presents rare species on a large proportion of patches and further has a high richness of rare species, can be named as 'most valued land-use type'. Several land-use types showed a high proportion of patches that contained rare species, especially at Frankenalb and Grafenwöhr. However, several land-use types were recorded on only few patches, as can be seen from the example of the land-use 'rock' at Frankenalb. There, the only recorded patch presented two red-listed species. For assigning this patch as very valuable, one would need further rock patches to be sampled. However, as can be seen from the example of 'fallow land' at Grafenwöhr, 86% of the 198 patches presented a number of 45 different threatened and endangered species. Noteworthy, at least 55% of all land-use types contained of one or more threatened and endangered species at GTA (Figure 4-8).

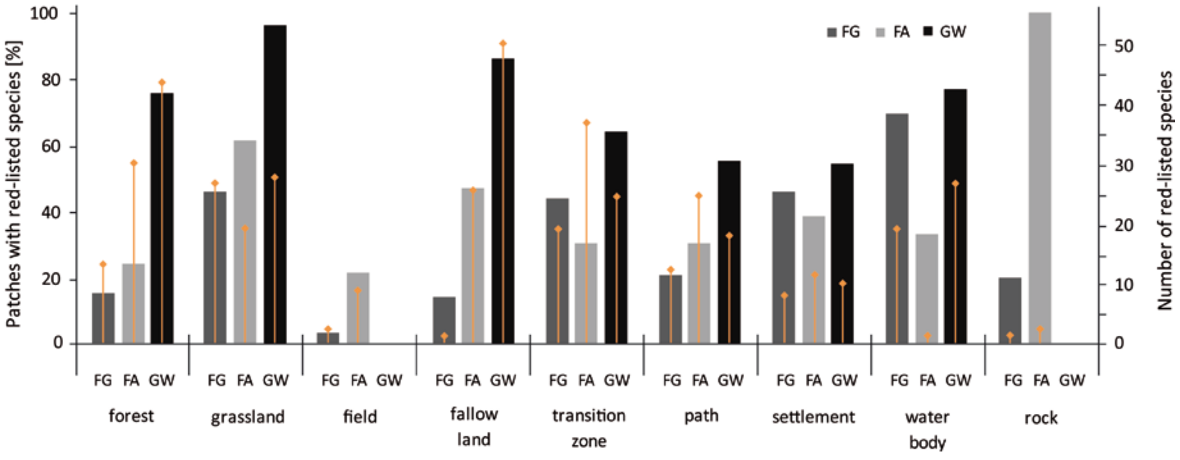


Figure 4-8: Value of land-use types: Left scale displays the occurrence of patches with red-listed species on certain land-use types (left scale, marked with bars). Right scale displays the total number of different red-listed species (=species richness) on same land-use types (marked with orange dots).

H3) Military training increases the number of alien plant species. They are distributed all over the area whereas in agricultural landscapes we find alien species along roads and on road margins.

The total number and percentage of alien species indicates a higher number in the agricultural landscapes than in the military training area. Both Frankenalb and Fichtelgebirge had 6.2% neophytes, whereas Grafenwöhr had 4.8% (Table 4-3).

Table 4-3: Number and proportion of non-native species within total species number which was higher in the agricultural landscapes than at the military training area.

	Species richness	No. of neophytes	Neophytes (%)
FG	404	25	6.2
FA	609	38	6.2
GW	620	30	4.8

The distribution of alien species in the military ground showed three important land-use types, i.e. fallow land (32.5%), paths (21.4%) and grassland (18.9%). Observing the most important disturbance types related to alien species, we found that ‘compaction by tracked vehicles’ (18.2%), ‘compaction by wheeled vehicles’ (23.5%), ‘foreign material’ (12.0%) and ‘gravel’ (9.0%) displayed exactly these areas where military training took place. Paths include the compaction by wheels and tracks and gravel, also characterized as ‘foreign material’, and are facility between the different training sectors. Military training takes place on fallow land and grassland. Other disturbances in these habitats, like mowing or macroherbivory, played a minor role.

At the agricultural landscapes, highest number of alien species was expected along roads and on road margins. The first category is named ‘path’, the road-margins are a sub-category of the land use ‘transition zones’. At Fichtelgebirge, more than 50% of road, field, grassland, settlement and rocky patches had one or more non-native species. Out of all alien species, 24% were found on roads and road margins. At Frankenalb, 70% of field patches and 75% of all settlement patches had non-native species within their species pool, as well as the only rocky patch. In total, 23% of all non-native species were found at roads and road margins (Figure 4-9).

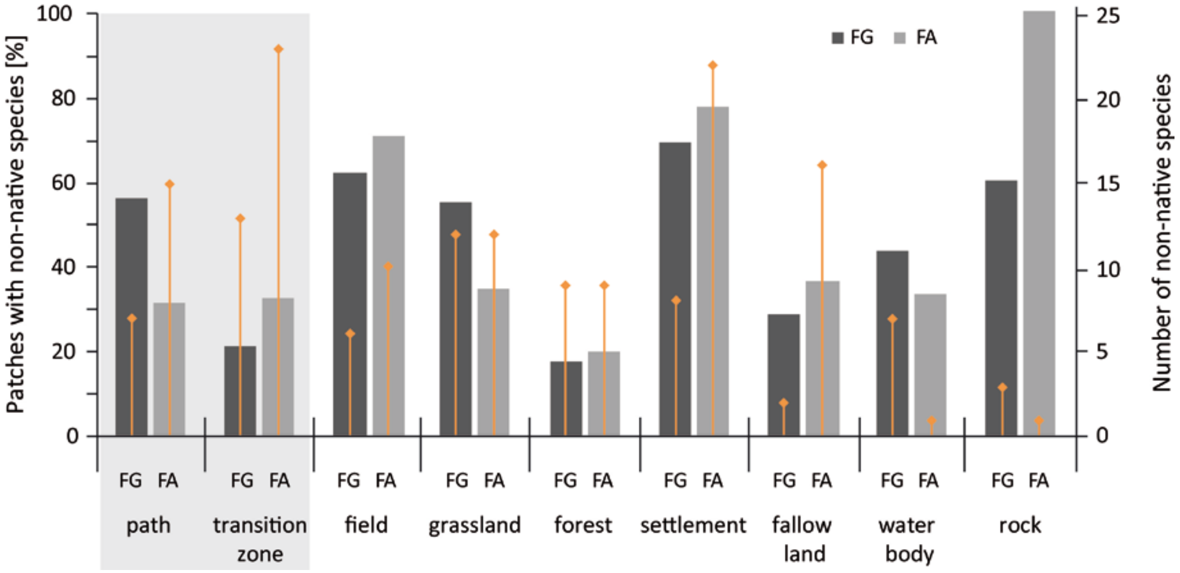


Figure 4-9: According my hypothesis, most alien species in the agricultural landscapes are found along roads and on margins. Figure shows comparison between the two agricultural landscapes. Left scale shows proportion of patches with alien plant species, right scale show absolute number of species. Grey field indicates roads and margins, where highest was expected. However, only one third of non-native species were found as expected.

Why did we find so many patches with alien species on fields, grassland and settlement? Are these several different or few but very frequently occurring species? Within the non-native species in both agricultural landscapes, fields and paths were dominated by *Matricaria discoidea* and *Veronica persica*. *Matricaria discoidea* is a ruderal strategist with the need for nitrogen (N=8) and light (L=8). *Veronica persica* is a cr-strategist and typically be found in fields and short-lived weed vegetations (L=6, N=7) (BfN). At Fichtelgebirge, grasslands were dominated by *Lolium multiflorum*, mostly found in wet meadows and pastures. At Frankenalb, *Galium mollugo* was the most identified species. Settlements, however, were not dominated by a certain species. Within the nine settlement patches at Fichtelgebirge, eight non-native species were identified, whereas at the 24 patches at Frankenalb, 22 non-natives were found.

Corresponding to the consistent land-use types, agricultural disturbances (FG: 21.5%, FA: 12.7%) and compaction by wheeled vehicles (FG: 28.9%; FA: 16.7%) were the major drivers for non-native species in fields. At Frankenalb, the application of pesticides was correlated with non-native species (27.9%). At Fichtelgebirge, the disturbance due to mowing (24.8%) had the biggest influence.

H4: High disturbance supports generalists, such as alien species. They are characterized by low seed weight, and seed production (=high distribution capacity), short life-cycle (annuals) and wind dispersal.

According to Arévalo *et al.* (2010), the replacement of the native flora by non-native or widespread species leads to homogenization of a landscape. The analyses of the influence of disturbance intensity on alien species numbers showed two different tendencies for forests and open landscapes. Forests showed a decreasing number of non-natives with increasing intensity. In contrast, the open landscape showed an increase at intermediate level, but a small decrease at high disturbance level (Table 4-4).

Table 4-4: Occurrence of non-native species in combination with disturbance intensity in forests and open landscape. Forests showed a decreasing number of non-natives with increasing intensity. The open landscape showed an increase at intermediate level, but a small decrease at high disturbance level.

Forest	**Neophytes (%)**	**Species richness**
Low	6.7	792
Intermed	2.9	509
High	3.0	528

Open landscape	**Neophytes (%)**	**Species richness**
Low	7.0	756
Intermed	7.8	699
high	6.8	735

Homogenization does not only affect species, but also functional traits and genotypes (Olden 2006; Olden & Rooney 2006). Therefore, the characteristics would be a fast regeneration and fast reproduction. Hence, as parameters for generalization were considered a) the number of biotopes where a species were recorded, b) the number of seed that is produced (high seed number = a high reproduction rate and therefore a high competition for space and nutrients), c) a low seed weight (maximizes the possibility of distribution by wind), and d) the strategy of using wind as dispersal vector (Figure 4-10).

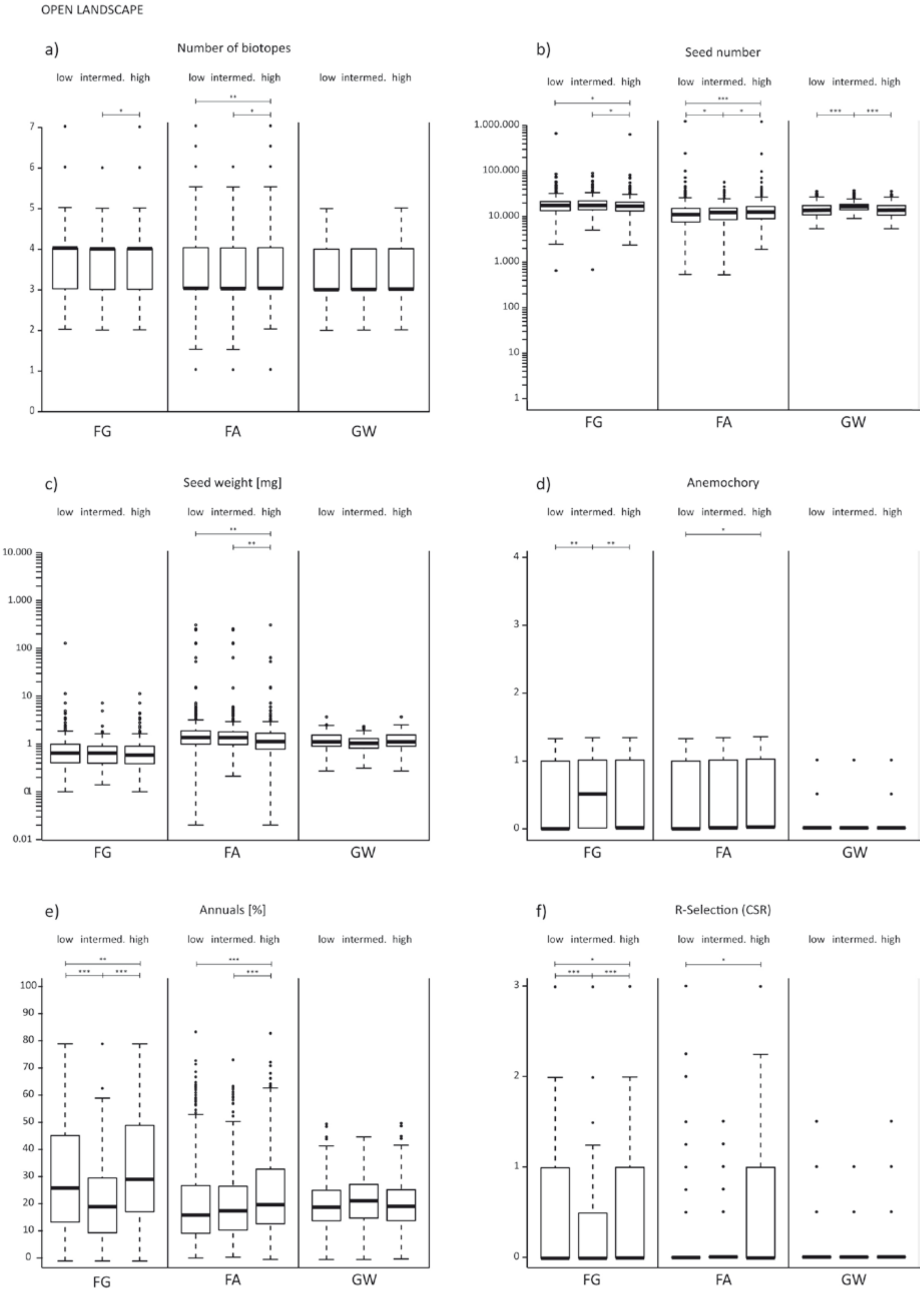


Figure 4-10: Analyses of functional traits and their changes along a disturbance intensity gradient. A) number of biotopes; b) seed number; c) seed weight, d) anemochory, e) annuals, f) R-Selection. Boxplots show open landscape data.

a) Number of biotopes

The number of biotopes, in which species occur, is an indicator for their specification. If they occur in just one habitat, they would be highly specialized, whereas a species that is found in several biotopes is classified as generalist. Analyses with open landscape data at Frankenalb showed a marginal but significant increase between low and high disturbance intensity and intermediate and high intensity, respectively. Fichtelgebirge showed a low significance between intermediate and high disturbance intensity. In forest patches, however, Fichtelgebirge showed a narrowing of biotope range at higher disturbance levels (50% box above 3 biotopes with high disturbance intensity), but with fewer specialists. At Frankenalb the range widened with additional specialist plant species. At the military training area, there were no significant differences.

b) seed-number

At Fichtelgebirge, there was a significant increase of seed numbers with increasing disturbance intensity. At Frankenalb, the seed production showed a highly significant increase with the increasing disturbance intensity. At Grafenwöhr, the differences between low and intermediate level and intermediate and high level were highly significant, with a peak of seed numbers at the intermediate disturbance level. Forests at Fichtelgebirge showed a tendency towards a higher seed number, but without statistical significance. At Frankenalb, disturbance intensity led to a significantly increasing seed number. Grafenwöhr showed a peak on intermediate level, but without significance.

c) Seed-weight

At Fichtelgebirge and Grafenwöhr, no significant differences in seed weight were detected. In contrast, at Frankenalb the seed mass decreased highly significant with increasing disturbance intensity. However, several plant species are able to implement a double strategy and vary their seed weight (Zhang 1998). Light seeds enable a fast distribution by wind, whereas a higher seed weight would distribute the offshoot more local. A plant which has successfully gained a foothold does not need to invest in fast and long-distance dispersal. This would be the case, if with increasing disturbance analyses would show a bimodal shape. However, this was not the case in all three forest data sets.

d) Anemochory

The three study sites showed different strategies in comparison with disturbance intensity. Plant species at Fichtelgebirge showed a significant higher tendency towards wind dispersal at intermediate disturbance intensity than at low or high disturbance level. At Frankenalb, however, there was a significant increase in anemochory towards a higher level of disturbance intensity. Plant species at Grafenwöhr showed similar strategies regardless the disturbance intensity level.

A summary of the homogenizing effect of disturbance intensity shows the strongest effect at the agricultural landscapes. At Frankenalb, number of biotopes, seed number, seed weight and wind dispersal were according other studies in literature. At Fichtelgebirge, there was the tendency towards a homogenizing effect with seed number and wind dispersal. At Grafenwöhr, seed number and seed weight showed the predicted effect at intermediate level of disturbance but no effective effect when analyzing the gradient.

It was tested, if increasing disturbance intensity would lead to a tendency towards the double strategy of dispersal by wind (light seeds) and animals (heavier seeds). However, the frequency of anemochory decreased. Zoochory showed the same tendency, therefore the ratio between anemochory and zoochory did not change.

Table 4-5: Homogenization effect on the three study sites. Suggestions of literature versus own observations. Both agricultural landscapes showed a tendency towards homogenization, especially at Frankenalb.

Traits	**Number of biotopes**	**Seed number**	**Seed weight**	**anemochory**
Literature	**↑[1]**	**↑[2]**	**↓[3] ↑[4]**	**↑[5]**
FG	→	↑	→	↗↘ (→)
FA	↑	↑	↓	↑
GW	→	↗↘ (→)	↘↗ (→)	→

[1] (Devictor *et al.* 2008); (Chiron *et al.* 2010); (Clavel *et al.* 2011)
[2] (Klotz *et al.* 2002)
[3] (Barik *et al.* 1996); (Gomez-Garcia *et al.* 2009)
[4] (Rusterholz *et al.* 2009)
[5] (McIntyre *et al.* 1995); (Kleyer 1999); (Klotz *et al.* 2002)

If not the disturbance intensity is the major factor for homogenization but the agricultural land use, we should find further parameters that support these findings in these two landscapes and no effect at Grafenwöhr Training Area. These are a tendency towards annual plant species and R-strategists.

e) Annual plant species

Both agricultural landscapes showed a highly significant increase in annual plant species. At low disturbance level, Fichtelgebirge species pool had a proportion of 30% of annuals, whereas there were 20% at Frankenalb. The same proportion was calculated at Grafenwöhr Training Area. At high disturbance intensity level, Fichtelgebirge species pool consisted of 33% annuals and Frankenalb of 24%. The military training area did not show any tendency. In forest patches, all three data sets did not show any significant differences along the disturbance gradient.

f) R-selection

In both agricultural landscapes, there was a significant tendency towards R-selection. Fichtelgebirge plant species data increased by 16%, whereas Frankenalb even increased by 30%. No differences were found at the military training area (Table 4-6).

Table 4-6: According to the literature, agricultural land use increases the number of annual species and R-selection. Both agricultural landscapes (FA, FG) showed corresponding results, whereas the military training area did not.

Traits **Literature**	**Annual species** **↑ [6]**	**R-selection** **↑[7]**
FG	↑	↑
FA	↑	↑
GW	→	↗↘ (→)

[6] (Rowlands 1980); (Severinghaus *et al.* 1981); (Hirst *et al.* 2003); (Kotanen 2004); (Chalmers *et al.* 2005); (Storkey *et al.* 2012); [7] (Grime 1979); (Traxler 1997)

Both agricultural landscapes showed results according other studies in increasing proportion of annual and ruderal plant species. At Grafenwöhr, only the tendency towards more ruderal species was according to the literature.

4.4 DISCUSSION

H1) Military training area contains more rare species than the agricultural landscape

On first sight, I found two clear results that the military training area contains more threatened and endangered species than the agricultural landscapes. First, the conventional agricultural landscape presented significantly less threatened and endangered species (TES) than the more extensive agricultural landscape. Second, the extensive agricultural landscape had a similar number of TES as the military training area. The first result was expected, as it was proven in several scientific studies (e.g., Burel *et al.* 1998; Reidsma *et al.* 2006; Billeter *et al.* 2008). The second result surprises somehow because military training areas usually are considered as being especially species-rich (e.g., Naturstiftung David 2007; Warren & Büttner 2008a; Warren & Büttner 2008b; Jentsch *et al.* 2009). Consequently, a ranking was expected concerning the number of TES on the military training area (GW) > the extensive agricultural landscape (FA) > the conventional agricultural landscape (FG).

Yet, the hypothesis did not consider the continuity of TES but only the richness. In focusing on the frequency of occurrence of endangered species across the landscape, the military training area showed more than twice as many patches of high value than the two agricultural landscapes, with a total of 77%. Additionally, the average richness of endangered species per patch was significantly higher. This cannot be related to the species pool but presumably to further parameters.

Comparing the two agricultural sites with the military area, I discovered two phenomena. First, the number of endangered species correlated with the species pool, which was consistent with the results of GW. Second, the proportion of patches with one or more threatened species showed a small difference between the conventional (28%) and the extensive (34%) land use. The question arises, whether this difference is related to the more extensive land use or the bedrock effect, as we have seen in chapter three. Since the military training area has similar bedrock like Frankenalb but had a significantly higher frequency of endangered species, the reason might be the land use system. Though, my results showed that the richness of TES is linked to the total number of species and therefore does not seem to be influenced by land use and the related disturbances. Consequently, my hypothesis was rejected.

Luoto (2000) found an increasing number of rare species in agricultural landscapes, when anthropogenic disturbances were rather moderate. This was supported by Helsen *et al.* (2011), who validated this result on different scales (plot, site and region). On the other side, Kleijn *et al.* (2009) concluded that in a world of high disturbance and fertilizer application we might find the rare species in only little disturbed and nutrient poor areas, or, as it was stated by Grebe et al., in areas that are subject to traditional land management (Grebe & Bauernschmitt 1999, in White & Jentsch 2001). In contrast, Römermann *et al.* (2008) see a reduction in species diversity with high nutrient input, but refer to site characteristics as a more important factor for rare species. In general, rare species seem to be ubiquitous ("common to be rare" - Bratli *et al.* 2006); Tscharntke *et al.* (2005) identified every third to second species within a community as rare.

H2) The occurrence of rare species is linked to disturbance intensity, abiotic conditions, land-use type

The results of the first hypothesis did not give sufficient explanations, where to find threatened and endangered species and why to find them exactly where they occurred. There, we discovered that the number of threatened and endangered species is closely linked to the total number of species. My multivariate analyses showed similar results with threatened and endangered species (RL) as dependent variable instead of species richness (SR), however, with a minor explanation power. This is, because the target variable (RL) showed a narrower range of 0 to 13 rare species per patch, whereas the analyses with species richness (SR) ranged from 1 to 178 plant species. Still, significance of the variables remained stable. In summary, the PLS-R analyses showed a broad variance of potentially important factors that could influence rare species. These were mainly the abiotic conditions of the landscapes but they were also related to land-use and disturbance regime.

This issue can be considered from two angles. First, land-use parameters and abiotic factors enhance the number of threatened and endangered species. Second, land use and abiotic factors enhance the number of common species, which is closely linked to rare species number (i.e., species richness always contains a certain percentage of rare species).

If land use and abiotic factors enhance species richness, then we expect the creation of more niches. As side-effect, number of TES is increased. Alternatively, the created niches are of particular importance, like sites with extreme conditions that are rare, competition-poor and therefore ideal for rare species. Consequently, the total species number increases.

Disturbance intensity

Several studies report reduced species richness due to an increasing disturbance intensity (e.g., Haddad *et al*. 2008; van Meerbeek *et al*. 2014). While Monks & Burrows (2014) stress that common plant species can cope better with disturbances than endangered species, Luoto (2000), in contrast, states that rare species are supported in an intermediate disturbed system. However, the statistical inclusion of three different variables of disturbance intensity (category low, intermediate and high) did not show any correlation because most red-listed species were found in two or three different intensity levels.

There might be three reasons for this result. (1) An overlapping of multiple disturbance types and their linked temporal and spatial parameters was found in many patches, especially at the military training area. This can blur clear results. (2) The intensity levels were built from the available categories of the disturbance characteristics *frequency*, *duration* and *size*. For each characteristic, the lowest, intermediate and highest category was assigned to an intensity level (Table 4-7).

Table 4-7: Selected parameters for the three disturbance intensity categories (low, intermediate, high).

Disturbance level	frequency	duration	size
Low	1x/century 1x/decade none	<1 day none	¼ area linear/punctual none
Intermediate	1x/year 2 x/year 3 x/year	<1 month <1 week	½ area ¾ area
High	>3x/year steady intense steady diffuse	<1 year >1 year	4/4 area

Like this, a certain combination of disturbance characteristics can be linked to a certain land-use type. In some cases, the characteristics might be represented in two or even all three disturbance intensity categories. For example, a grassland which is mowed twice a year (intermediate frequency), with disturbance duration of less than one day (short-time impact) in its full extend (high extend of disturbance) shows characteristics of all three levels. (3) Organisms have a different threshold where disturbances show an effect which depends on their life cycle. As Fox (2013b) discussed in his paper, criticizing the IDH, it would be necessary to distinguish the intermediate level of disturbance in respect to the life-span and size of the organism observed. However, in this study I did not focus on the intensity of disturbance on a single plant species, but on the diversity of species of different life span like annuals, perennials or trees.

Abiotic conditions

Threatened and endangered species were found under nearly all abiotic conditions. Main driver - not only for the red-listed species, but also for overall species richness - was the pH value, or Ellenberg indicator value R, respectively. Hence it might be obvious, that this is due to the alkaline soils at Frankenalb and Grafenwöhr. However, the PCA did not show major differences between the siliceous landscape of Fichtelgebirge and the two study sites on calcareous bedrock. Therefore I assume, that it is not the habitat conditions that are the determining factors, but the local species pool.

High nitrogen input significantly minimized the number of rare species, as stated by Kleijn *et al.* (2009). In agricultural landscapes, nitrogen input is due to fertilization. At the military training area, besides the general atmospheric input (Bobbink *et al.* 1998) and probable wind loads from the surrounding agricultural fields, it might be the input of the ubiquitous animals (deer, wild boar) and their faeces (Marion *et al.* 2010). However, Wassen *et al.* (2005) showed that endangered species rather suffer under phosphorus enrichment than under nitrogen enrichment. A more general finding was declared by Kleijn *et al.* (2008), who saw the average rare species in a restricted variance (ecological amplitude) of abiotic parameters. Yet, the TES in the open landscape of Fichtelgebirge, Frankenalb and Grafenwöhr did not show this general pattern. Römermann *et al.* (2008) substantiated the conditions for rare species with preferences for "for warm, dry, light and nutrient poor conditions", which I compared with the findings of my study sites (Table 4-8).

Table 4-8: Comparison of own data with analyses of Römermann *et al.* 2008, who substantiated the conditions for rare species with preferences for "for warm, dry, light and nutrient poor conditions".

	Römermann *et al.* 2008	**Fichtelgebirge**	**Frankenalb**	**Grafenwöhr**
Warm (Ell-T)	↑	→	→	→
Dry (Ell-F)	↓	↑	↓	→
Light (Ell-L)	↑	↑	↑	↑
Nutrient poor (Ell-N)	↓	↓	↓	↓

All three study sites showed a shift towards lighter conditions and a significant preference for nutrient-poor conditions. Similar findings were confirmed by Gabrielová *et al.* (2013). Schön (1998) stated that due to these clear tendencies, light and nutrients do not show bimodal distributions. A temperature shift was not obvious. Only the species of Frankenalb showed a clear tendency towards dryer conditions, whereas at Fichtelgebirge and Grafenwöhr, the rather unimodal peak of humidity (F~5) showed a bimodal shape at F~4.5 and F~9 (FG) and F~3 and F~8.5 (GW), respectively (for differences of Ellenberg indicator values for rare and common species see S 4).

However, disturbance intensity did not change the variance of environmental parameters, but shifted only the peak. This means that no new niches are created. What can happen is that due to the shifting, the peripheral corners of the abiotic conditions become rare and therefore ideal for competition-poor rare species (e.g., remnant shaded areas, when vegetation is removed everywhere else).

Land use

A closer look at the TES supports these findings. Most of the rare species of Frankenalb were found on dry and nutrient-poor meadows ($F_{(mean)}$= 4.9; $N_{(mean)}$ = 3.3), on fallow land and along roads and were assigned to dry and semi-dry grasslands. Every fifth rare species was assigned to ruderal environment.

The endangered species of Grafenwöhr Training Area were recorded in a similar large share on dry grassland or fallow land, on disturbed ground as ruderal species and in forests with a higher humidity, especially due to water filled remnants of excavation sites for tank camouflage.

At Fichtelgebirge, TES were found either in grassland and wet meadows or along the banks of water bodies, which explains the bimodal shape. These water bodies were mostly fish ponds and rare species were found in 16 of 23 patches. But what makes the banks of ponds that species rich? The Ellenberg indicator values of several rare species did not only show high values for humidity but also for a higher pH than it is to be expected on siliceous bedrock. There might be two reasons for these unexpected basophile species. First, gravel made from limestone could have been used for bank reinforcement. Second, it is common practice to lime fish ponds in siliceous landscapes for disinfection and neutralization, to increase the nutrient availability (Lazur *et al.* 2010). This indicates that the niche quality (due to better environmental conditions) pushes rare species. If the number of rare species would be strongly connected to the species number, we should see a shift in total species richness under these conditions. Yet, the numbers were not correlated. This leads to the conclusion that bedrock actually does have an influence on the number of TES and furthermore explains the differences in my agricultural data sets.

Several studies compare both calcareous and siliceous bedrock and prove the differences in species richness (e.g., (Pausas & Carreras 1995); (Jentsch 2001); (Michalet *et al.* 2002); (Ewald 2003); {Piqueray 2007 #2483, but they either did not show a local calcareous influence in a siliceous area or they did not establish a connection to threatened and endangered species.

Threatened and endangered species were recorded not only in the open landscape but also in forests. I found differences of the number of TES along a land-use intensity gradient. Fichtelgebirge, as the study site with the most intense silviculture, showed the lowest number of rare species, whereas at the military training area with an only little anthropogenic impact in forests showed the highest diversity. Concerning species richness, this is confirmed by Paillet *et al.* (2009) who showed that unmanaged forests had higher plant species diversity than forest with higher impact. However, they point out the light as limiting factor. Therefore managed forests can be species rich if light is available (Antos 2009). However, these findings are related to species richness and not to the number of TES. Nevertheless, rare forest species showed a higher light affinity than the common forest species of my data. This was consistent in all three data sets. But can it be related to forest management? Graae & Heskjær (1997) did not find differences between the plant species diversity of managed and unmanaged forests. Gustafsson (2002) found more TES in unmanaged deciduous forests of northern Europe, but substantiated her findings with the need for dead wood and older stand age. The number of rare species at Grafenwöhr forests was three times higher than at Fichtelgebirge and nearly two times higher than at Frankenalb. Furthermore, the percentage of patches with red-listed species was three to four times higher than in the two agricultural landscapes, comprising nearly 75% of all forest patches. If rare species would be correlated to total species number and enhanced by bedrock, the numbers of TES at Frankenalb should be significantly higher than it was recorded. Therefore the forest management has the strongest influence on rare species.

H3) Military training increases the number of alien plant species. They are distributed all over the area whereas in agricultural landscapes we find alien species along roads and on road margins.

The total number of neophytes was smaller at the military training area than in the two agricultural landscapes. Therefore the expectation that military training acts as a gateway for non-native plant species, had to be rejected. Nevertheless, troop transports bear a high risk of unintentional transported seeds. Nentwig (2008) delineated a different control system for international military transports which would be more risky towards unintentional passengers, like seeds, plants or animals. Grafenwöhr Military Training Area is one of the biggest training areas in Europe and serves as hub for international military operations. Therefore it was expected that the international transport of military equipment would lead to an increasing input of non-native plant species. The U.S Department of Agriculture (USDA) and the Department of Defense (DoD) conducted several scientific studies in a natural resource conservation program (Boice 2010) to be able to cope with these risks. A study of the National Wildlife Federation on military training installations revealed such a big impact of alien species that costly conservation was necessary to protect endangered species and their habitats on nine of 12 study sites (Westbrook & Ramos 2005). Furthermore they found out that the quality of military training was directly affected, for example by the long spines of the yellow star-thistle *Centaurea solstitialis*. In 2007, the DoD finally published a guidebook with instructions how to clean the equipment (Cofrancesco *et al.* 2007).

At Grafenwöhr Training Area, the distribution of neophytes was clearly related to the military actions. Several alien species were found within the areas where direct training occurs. As vectors, tracked and wheeled vehicles come into question (Taylor *et al.* 2012). Yet, also the infrastructure plays an important role, like on gravel roads. Within the sampled transition zones, 50% of all non-native species were found in the mounds (gravel core covered with soil) along the roads. These mounds are used for tactical training (hidden driving) and prevent dust plumes from the dry gravelled roads.

Most neophytes are found in habitats under the influence of anthropogenic disturbances, like ruderal habitats and along traffic routes, whereas indigenous species are found in low to moderate disturbed areas (Kotanen 2004; Kowarik 2010; Nehring *et al.* 2013; Jauni *et al.* 2014). In a meta-analysis, Jauni *et al.* (2014) found out that after disturbance, alien species responded with increasing diversity and abundance, whereas the native species did not.

In both agricultural landscapes, every fourth non-native species was recorded along roads and road margins. However, non-native species were found in all land-use types. At Fichtelgebirge, mostly roads, fields and grassland showed highest proportion of alien species, whereas they were more distributed in Frankenalb. There, settlements showed a remarkably high number of alien species. In comparison to Fichtelgebirge, more settlement patches were recorded. The distribution of non-native species starts with garden escapes and garden throw-outs (Hodkinson & Thompson 1997; Kowarik 2010). One of these escapes is *Matricaria discoidea* (wild chamomile). It is classified as introduced neophyte. It was found on 39% of all recorded non-native relevés at Fichtelgebirge and on 15% of the records of Frankenalb. Oberdorfer (2001) classifies its habitat near settlements and as indicator for nitrogen input. Besides the pineappleweed, *Lolium multiflorum* was found in 18% of the records. It can perfectly cope with fertilization, grazing and frequent mowing. These two species cover nearly 60% of all alien species recording at Fichtelgebirge. At Frankenalb as much as at Grafenwöhr, however, more alien species with less abundance were found.

H4) High disturbance supports generalists, such as alien species. They are characterized by high seed weight, and seed production (=high distribution capacity), short life-cycle (annuals) and wind dispersal.

According to Büchi & Vuilleumier (2014), most non-indigenous species are generalists and are found in more than one habitat. Their dispersal ability is more effective (Fried *et al.* 2010) and they are adapted or at least they can cope with the biotic and abiotic circumstances in different environments. Several studies report an increasing number of generalist plant species and alien species due to land-use change or disturbances (Deutschewitz *et al.* 2003; Devictor *et al.* 2008; Arévalo *et al.* 2010; Chiron *et al.* 2010; Clavel *et al.* 2011; Stohlgren *et al.* 2011; Jauni *et al.* 2014; van Meerbeek *et al.* 2014). This effect, of replacing more specialist species by the more general species homogenizes a landscape and makes it more similar to the adjacent habitats (Naaf & Wulf 2010).

All of our sampled study areas exhibited exotic species, whereas a higher number was found in the agricultural than in the semi-natural landscape. However, they were widely distributed in all kinds of land-use types. Estimations suggest around 12,000 alien higher plant species in Germany (Kowarik & Boye 2003). Some 600 count as established; only 30 of them show invasive habits (Klingenstein *et al.* 2005). According to Kowarik (2010), most alien species occupy highly disturbed areas, whereas native plant species are rather found on low to moderately disturbed grounds. High disturbance intensity increases the number of generalist species, because disturbances function as a filter for specialist plant species. Furthermore, disturbances directly enhance the homogenizing effect (Abadie *et al.* 2011). According to the definition of Olden (2006), biotic homogenization is measured in observing the “change in pairwise similarity between two time periods”. Since our study sites have not been resampled, my approach was to determine the differences in species occurrence and life history traits along a disturbance intensity gradient.

My results showed a clear tendency towards homogenizing effects at the two agricultural landscapes, especially at Frankenalb, where traits changed with increasing disturbance intensity towards a faster and more effective dispersal strategy. At Fichtelgebirge, number of biotopes and seed number showed similar effects like at Frankenalb, whereas seed weight and the dispersal strategy for wind dispersal did not show that clear tendencies. No or probably only a weak effect was found at Grafenwöhr Training Area. But what makes these effects and why do we find these differences?

At Grafenwöhr, the high number of local species seems to buffer the influence of the non-native species. According to Catford *et al.* (2012), the evolution of a species within its environment might limit the ability to cope with novel disturbances. Since Grafenwöhr undergoes frequent and undirected disturbances in the areas that would be most affected by alien species, the native species seem to exhibit a “greater breath in functional space” (Olden *et al.* 2004) and are able to cope with the invaders. In contrast, species in the agricultural landscapes might be comfortable in their habitats with repeatedly occurring disturbances and sufficient nutrient supply. Because introduced species are adapted to anthropogenic disturbances (Kowarik 2008), they seem to be a challenge for the local communities.

On the other side, despite the missing clear effects of some traits, both landscapes showed a higher amount of annual species and the tendency towards the R-strategy. In agricultural landscapes, arable weed vegetation also shows these characteristics.

In summary, the agricultural landscapes show a similar tendency towards the expectations of increasing numbers of generalist plant species and several life history characteristics. Therefore for the agricultural landscape, the hypothesis that disturbance supports generalist plant species and therefore enhances the homogenization of a landscape was confirmed. In contrast, the results of the military training area were less clear or often converse. Therefore, the hypothesis was rejected for the military training area. In forest patches, all three data sets did not show any significant differences along the disturbance gradient.

The military training area of Grafenwöhr seems to be the ideal landscape. It presents a tremendous plant diversity, a diverse landscape with a large variety of habitats, but still offers space for anthropogenic activities without major restrictions. Furthermore, the environment seems stable regarding invaders and homogenization. It should therefore be a goal to put more military training areas under protection because of the sustainability of the land use (Gazenbeek 2006; Warren *et al.* 2007).

Admittedly, the land-use system of a military training area cannot be simply imposed on an agricultural landscape that is needed to assure food supply. However, in case of Frankenalb as intermediately positioned in between the more intensively and the more naturally maintained landscapes, an optimization, especially towards organic farming would improve and strengthen the local plant communities.

Chapter 5

5 SYNTHESIS

The intention of my thesis was to explain phytodiversity under the influence of land use and disturbances in a cultural landscape. To ensure maximum objectivity as many disturbance parameters as possible were sampled and included into the analyses. The three analyzed study sites belong to the same ecoregion and are subject of similar climatic conditions due to their geographic proximity. They mainly differ in two characteristics, land use and bedrock. Fichtelgebirge (FG) and Frankenalb (FA) are characterized by agricultural land use, whereas Grafenwöhr (GW) is used for military training. Fichtelgebirge is situated on siliceous bedrock, though Frankenalb and Grafenwöhr Training Area are located within a calcareous landscape. Furthermore, the three study sites display three different land-use intensities. At the military training area, heavy damages can occur during the training activities, but in the same time, large areas are maintained in a natural to semi-natural state. Frankenalb is used for extensive agriculture, with smaller fields and pastures, whereas at Fichtelgebirge, more intensive agriculture on larger-sized fields and meadows dominates the landscape. Forests in the agricultural landscapes are shaped by modern silviculture, whereas in the military training area, a semi-natural silviculture is practiced and nearly untouched areas are frequent. Therefore forests at Grafenwöhr are much sparser.

Military training areas count as very species rich due to their semi-natural maintenance. This, in addition to the positive aspects of basic soils, led to the expectation that the diversity would be highest at Grafenwöhr. These aspects counted also for the second study site on limestone, Frankenalb, since the extensive land use allows more semi-natural habitats. But due to agricultural land use, in particular field management and the application of fertilizers, a reduced number of species was expected. At Fichtelgebirge, the more intensively managed fields and meadows and the disadvantage of acidic ground reduced our expectations of high species richness. Similarly, it was expected to find more threatened and endangered species on the military ground, as their occurrence is referred to the heterogeneity of a landscape (e.g., Helsen *et al.* 2011; Warren *et al.* 2007; Cizek *et al.* 2013; Warren & Büttner 2014).

Total species numbers (γ-diversity) did not exactly show the expected order of GW>FA>FG, because of a slightly higher species richness at Frankenalb. Still, on plot level, the richness of Grafenwöhr and Frankenalb was about one third higher than the species diversity at Fichtelgebirge. The presence of threatened and endangered species showed a similar pattern, but with a slightly higher number in the military training area. The ratio to those at Fichtelgebirge was similar to the number of total diversity.

Observations changed on patch level (α-diversity), where both agricultural study sites showed nearly similar, but significantly lower richness of total species as well as rare species compared to the military training area. For both species categories the less intensely managed landscape Frankenalb showed slightly higher values than Fichtelgebirge. At first sight, these results appear contradictorily, but they show two findings. The first finding is that the scale of observation is important. The second finding is that total species richness and number of threatened and endangered species are correlated.

On plot scale, bedrock seemed to have highest influence on species richness. Both study sites situated on limestone presented highest total species richness. Moreover, land use was of further importance. At Frankenalb and Grafenwöhr, the semi-natural habitats showed highest species richness and highest number of threatened and endangered species.

A further aspect was the heterogeneity of the landscape. On plot scale, it was expressed as the variety of land-use types, disturbance types and designated patches. The heterogeneity was positively correlated to species richness. One hectare plots with one land-use type only, showed less species than plots with several different land-use types and disturbance regimes.

A further difference within the two agricultural landscapes was the number and size of designated patches. Fichtelgebirge had larger-sized fields and meadows, whereas land-use types at Frankenalb were smaller scaled. As a consequence, the type of maintenance changed more frequent. Grafenwöhr had patch sizes in the range of the Fichtelgebirge data, but the disturbance regime was much more heterogeneous because of a higher number of disturbance types and overlapping disturbances within one site that did not allow the designation of further patches.

The three landscapes showed significant differences in their forests. In contrast to the two agricultural landscapes, forests at Grafenwöhr pushed species numbers in an unprecedented dimension and disturbance parameters related to forestry dominated the analyses on plot scale. Similar pattern were derived with the analyses of threatened and endangered species. Reason might be a sparser tree population which allows more light available for the understory (Elemans 2004). Additionally, the natural to semi-natural maintenance of large proportions of the forests offer a variety of habitats, for example on lying deadwood.

While on plot scale bedrock, land use and land-use heterogeneity explained (much of the) species richness, analyses on patch scale indicated that there must be further important parameters: An influence of pH (Ellenberg-R) was significant, further important abiotic parameters improved the explanation for species richness, i.e. light, nutrients and humidity. Mostly either the maximum values or the variance (max-min) of the abiotic parameters showed significance. If one considers a high diversity of niches one finds small-scaled environmental heterogeneity, including soil conditions and light availability. An effect was discovered around ponds at Fichtelgebirge, where calcicoles clustered, most probably because of liming of the water. However, this effect rather increased the number of rare species but not the total species richness which suggests that rare species react on small-scaled abiotic changes.

As shown in several publications and supported by my data, the military training area was very heterogeneous. The multiple disturbances, i.e. overlapping anthropogenic and natural influences, create a landscape mosaic of undisturbed to extremely disturbed areas as well as habitats in all phases of succession. Another kind of small-scaled heterogeneity was shown by the extensive agricultural landscape of Frankenalb. Frequently changing land use led to the designation of nearly double number of patches than at Grafenwöhr and at Fichtelgebirge. However, regressions showed that plots with highest patch heterogeneity did not necessarily have highest species number. A recently published study, conducted at a similar scale in forests of the French Alps, dealt with this phenomenon (Redon *et al*. 2014). They assumed that at highest heterogeneity species richness starts to decrease again, because this level of heterogeneity is a synonym for fragmentation. Finally they admitted that there was no proof for this hypothesis and referred to further driving factors. In the case of the species decay in my data, a reason might be that we reached the limit of the species pool. Niches are saturated and therefore not available anymore, which reduces species number. However, since we find species numbers beyond this certain level, this explanation is unlikely. Therefore it seems just coincidence which we cannot prove, because of missing replicates.

In the case of Grafenwöhr and Frankenalb, this question can be picked up again, since both show identical species numbers. While at Grafenwöhr the landscape was open and heterogeneous by intermingling disturbance under similar environmental conditions, Frankenalb was separated by forests and small-scaled open land-use types. Which landscape might first be affected by the negative consequences of fragmentation? To find a solution, my suggestion is to take abiotic conditions into account which should differ more in the agricultural than in the military area.

To understand community dynamics, disturbance intensity has to be taken into account. The three study sites showed a broad variation of disturbance types and related temporal and spatial characteristics. I calculated three disturbance levels (low, intermediate, high) to analyze their influence on species richness, threatened and endangered species and on non-native species. According to the Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978) and numerous studies, species richness is maximized at intermediate level of disturbance. This is because at low disturbance intensity competitive exclusion and the dominance of long-lived species reduce species diversity. Though at high intensity, only fast colonizers are successful (Huston 1979). At intermediate level, both strategies are possible and therefore enhance richness. My results showed no effect of the Intermediate Disturbance Hypothesis on total species richness which actually was not unexpected. Analyzing a community for indicators towards the IDH presupposes species with a similar life span. My study focused on the intensity of disturbance on the diversity of species of the whole community including species of different life span like annuals, perennials or trees. We have to assume a certain intensity gradient that a species can deal with and a threshold when a species cannot tolerate a disturbance anymore. The levels of disturbance intensity have to be adjusted to this gradient, which, logically, differs much between annual species and long living trees (Shea *et al.* 2004).

Furthermore, disturbance can lead to an invasion of non-native species (McIntyre & Lavorel 1994). In our globalized world there are numerous ways how non-native species can be introduced. In agricultural landscapes, main vectors are uncleaned seed mixtures or offsprings from ornamental plants in gardens. At military training areas, the main vector is contaminated material from international troop transports. The agricultural landscapes presented six percent and the military landscape five percent of alien species in their species pools. Nevertheless, despite the moderate numbers, they were ubiquitous. At the agricultural landscapes, most aliens were found on field and settlement patches and along roads. At the military training area, they were found along roads, on grassland and on fallow land. Even if the military actions did not function as the expected gateway for alien species (Westbrook & Ramos 2005; Cofrancesco *et al.* 2007), the distribution within the area was clearly related to the maintenance of the site and the military training itself.

The ecological value of a landscape tends to be measured according to its species richness and the number of rare species (Humphries *et al.* 1995). In general, native species are protected whereas neophytes are despised. In fact, many agricultural crop plants were introduced as well, but were naturalized in the meantime (archaeophytes) and are very common. Like native species and archaeophytes, also neophytes enhance species spectrum and biodiversity (Sax & Gaines 2003). The difference is that neophytes may promote biotic homogenization, which is no regional phenomenon anymore but has become a global problem. Homogenization induces changes on species level and alters functional traits and genes (McKinney & Lockwood 1999; Baiser & Lockwood 2011). A reduced gene pool affects the whole community and implies a reduced stability and resistance to environmental change. In the extreme, existing communities can be completely exchanged by invaders. Catford *et al.* (2012) stated that native species are adapted to the consisting disturbance regime due to their history. In case of new disturbances, probably the ones that introduce non-native species, they would be disadvantaged and outcompeted by the introduced species. Referring to the IDH, they concluded that there might be two different disturbance intensity levels that maximize species richness, i.e. one for native and one for non-native species.

My data showed that the land use appears to be the decisive factor, because the landscapes show different reactions, despite the nearly identical low portion of neophytes. A tendency towards biotic homogenization was found in the agricultural landscapes, whereas the military training area did not show significant changes along the disturbance gradient. The frequent and undirected disturbances that can occur at any time of the year seem to broaden the functional space of the native community (Olden *et al.* 2004). This, and a high species richness, provide stability against possible invaders. In contrast, agricultural landscapes undergo a regular shaping at certain time periods and frequencies. Plant species might be adapted in a narrow, because sufficient functional space. Novel disturbances and introduced species therefore seem to influence the (anyway small) community.

The extent of my thesis underlines the complexity of nature with such a high quantity of interactions that it is very difficult to filter and to find easy and clear answers. For that reason, most ecological studies pick out few parameters to study the effects when changing them. But there might be occasions where a key parameter is missing. This I realized when I conducted the multivariate statistics on patch level. As soon as I included abiotic parameters, the explanation significantly increased. Therefore, the advantage of my study is the unique complexity of disturbance parameters.

Outlook

The military training area seems to be the ideal landscape. It presents a high taxonomic and functional diversity on all scales, threatened and endangered species not only in all land-use types but also in high abundance, and stability in face of neophytes. Yet, we have to consider, that Grafenwöhr Training Area is located in a cultural landscape. A large and dense population, like we find in Germany, needs space for agricultural land use. As numerous studies prove, agricultural impacts show very negative effects on biodiversity but also on water quality and greenhouse gas emission, caused by fragmentation, fertilization and simplification of the landscape during the last 50 years.

My results further revealed that species richness and the number of threatened and endangered species are correlated. For conservational actions we consequently need to ask how much effort is necessary and useful to focus on a few species of high ‘value’. Would it not be easier and cheaper to simply enhance total diversity which in turn would be very likely to the detriment of some species?

Green (2005) presents two options of how to protect a landscape. The first option is a “wildlife-friendly farming”. It results in a high diversity but reduces agricultural yields. In turn, a larger farmed area would be needed to cope for the reduction. The second option is a “land-sparing” system. It results in the intensification of agricultural impacts on smaller fields and the protection of the remaining areas. Myers *et al.* (2000) point out that it is impossible to protect all species. They suggest to identify hotspots and to put all effort into them. As a consequence, Meyer *et al.* would probably select the second option, whereas traditional nature conservationists probably would tend towards option one.

However, this question has to be regarded in a more differentiated way according to the regional circumstances. Imagine that parts of Frankenalb would be managed Grafenwöhr-like resulting in a higher species richness in those patches. These patches would present not only a high variety but also a high abundance of rare species, which emphasizes their value as reserve. Since the two areas share several threatened and endangered species, it would naturally protect the bulk of plants at Frankenalb. With this scenario, it would be conceivable to choose option two.

Species richness on military training areas has emerged by chance and species numbers would not be that high without the disturbance caused by the training. In ceasing the activities, competition leads to a decrease of species diversity. Therefore, big efforts and a lot of money are necessary to preserve abandoned training areas as open landscapes (Jentsch *et al.* 2009; Cizek *et al.* 2013).

Today, many farms are subsidized to conduct extensive agriculture on single plots. Farmers more and more undertake task concerning nature conservation. Still, in many regions farming has been abandoned because it did not pay off anymore. An ideal way to protect valuable landscapes would be to pay farmers as professional caretakers for a sustainable management.

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III. SUPPLEMENT

S 1: List of land-use and disturbance parameters, used for multivariate statistics. 'No.' = consecutive number, 'variables short' = condensed label, 'variable explanation' = description of condensed label.

No.	Variables short	Variable explanation
	general information	
v001	GW	Grafenwöhr Training Area
v002	FA	Frankenalb (extensive agriculture)
v003	FG	Fichtelgebirge (intensive agriculture)
v004	SR	number of species per patch
v005	RL	number of red-listed species per patch
v006	size/m²	patch size [m²]
	heterogeneity	
v007	no.diff.patch	number of patches per plot
v008	no.diff.landuse	number of different land uses per plot
v009	no.diff.disttypes	number of different disturbance types per plot
v010	no.diff.freq	number of different frequencies per plot
v011	no.diff.seas	number of different seasons per plot
v012	no.diff.dur	number of different durations per plot
v013	no.diff.size	number of different sizes per plot
v014	no.diff.form	number of different forms per plot
v015	no.diff.distr	number of different distributions per plot
v016	no.diff.sel	number of different selectivities per plot
	land-use types	
v017	lu.fallowland	fallow land/succession
v018	lu.field	field
v019	lu.forest	forest
v020	lu.grassland	grassland
v021	lu.misc.constr.	miscellaneous constructions
v022	lu.path	path
v023	lu.rock	rock
v024	lu.settlement	settlement
v025	lu.transitionzone	transition zone
v026	lu.waterbody	water body
	disturbance types	
v027	dist.agriculture	agriculture
v028	dist.biomass.export	biomass export
v029	dist.biomass.input	biomass input
v030	dist.breakage	breakage
v031	dist.clearfelling	clear felling
v032	dist.compaction.tracks	compaction (tracks)
v033	dist.compaction.trampling	compaction (trampling)
v034	dist.compaction.wheels	compaction (wheels)
v035	dist.contamination	contamination
v036	dist.creekrealloc	creek reallocation
v037	dist.deadwood	deadwood collection
v038	dist.dehydration	dehydration
v039	dist.depression.waterfilled	depression (water filled)
v040	dist.erosion.water	erosion (water)
v041	dist.excavation.open	excavation (open)
v042	dist.farm	farming
v043	dist.fencing	fencing
v044	dist.gardening	gardening
v045	dist.fire	fire
v046	dist.flooding	flooding
v047	dist.foreign.material	foreign material
v048	dist.gravel.basalt	gravel (basalt)
v049	dist.gravel.lime	gravel (lime)
v050	dist.grovefelling	grove felling
v051	dist.hydraulicengineering	hydraulic engineering
v052	dist.leveling	leveling

v053	dist.macroherbivory	macroherbivory
v054	dist.materialstoring	material storing
v055	dist.microherbivory	macroherbivory
v056	dist.mowing	mowing
v057	dist.none	none
v058	dist.nutrientinput	nutrient input
v059	dist.pesticides	pesticide application
v060	dist.pond.drainage	pond-drainage
v061	dist.quarry	quarry
v062	dist.rejuvenation	rejuvenation
v063	dist.sealing	sealing
v064	dist.seeding	seeding
v065	dist.single.treefelling	single tree felling
v066	dist.skiddingtrack	skidding track
v067	dist.soil.rock.movements	soil and rock movements
v068	dist.thinning	thinning
v069	dist.wildboar	wild boar damages
v070	dist.woodstorage.movement	wood storage or movement
	disturbance frequency	
v071	freq.1x.century	once per century
v072	freq.1x.decade	once per decade
v073	freq.1x.year	once per year
v074	freq.2x.year	twice per year
v075	freq.3x.year	three times per year
v076	freq.>3x.year	more than three times per year
v077	freq.steadydiffuse	steady diffuse
v078	freq.steadyintense	steady intense
v079	freq.none	none
	disturbance seasonality	
v080	seas.1q	1st quarter of the year
v081	seas.1-3q	1st to 3rd quarter of the year
v082	seas.1-4q	all year round
v083	seas.1&4q	1st and 4th quarter of the year
v084	seas.2q	2nd quarter of the year
v085	seas.2-3q	2nd to 3rd quarter of the year
v086	seas.2-4q	2nd to 4th quarter of the year
v087	seas.3q	3rd quarter of the year
v088	seas.3-4q	3rd to 4th quarter of the year
v089	seas.4q	4th quarter of the year
v090	seas.none	none
	disturbance duration	
v091	dur.<1day	less than 1 day
v092	dur.<week	less than 1 week
v093	dur.<1month	less than 1 month
v094	dur.<year	less than 1 year
v095	dur.>1year	more than 1 year
v096	dur.none	none
	disturbance size	
v097	size.1.4.area	1/4 of the patch
v098	size.1.2.area	1/2 of the patch
v099	size.3.4.area	3/4 of the patch
v100	size.4.4.area	full patch
v101	size.linpunct	linear or punctiform
v102	size.none	none
	disturbance form	
v103	form.laminar	laminar
v104	form.linear	linear
v105	form.punctual	punctual
v106	form.none	none

	disturbance distribution	
v107	distr.heterog	heterogeneous
v108	distr.homog	homogeneous
v109	distr.none	none
	disturbance selectivity	
v110	sel.age	age
v111	sel.loc	location
v112	sel.spec	species
v113	sel.age.loc	age & location
v114	sel.age.spec	age & species
v115	sel.age.spec.loc	age & species & location
v116	sel.spec.loc	species & location
v117	sel.lot.boundary	lot boundary
v118	sel.none	none
	intermediate disturbance	
v119	IDH.quant	quantitative IDH
v120	IDH.x	disturbance intensity higher than IDH spectrum
v121	IDH.0	none of three parametersin IDH spectrum
v122	IDH.1	one of three parameters in IDH spectrum
v123	IDH.2	two of three parameters in IDH spectrum
v124	IDH.3	three of three parameters in IDH spectrum
	Ellenberg indicator values	
v125	F.min	Ellenberg moisture minimum
v126	F.max	Ellenberg moisture maximum
v127	F.med	Ellenberg moisture median
v128	F.maxmed	Ellenberg moisture difference maximum-medium
v129	F.maxmin	Ellenberg moisture difference maximum-minimum
v130	L.min	Ellenberg light minimum
v131	L.max	Ellenberg light maximum
v132	L.med	Ellenberg light median
v133	L.maxmin	Ellenberg light difference maximum-minimum
v134	N.min	Ellenberg nitrogen minimum
v135	N.max	Ellenberg nitrogen maximum
v136	N.med	Ellenberg nitrogen median
v137	N.maxmed	Ellenberg nitrogen difference maximum-medium
v138	N.maxmin	Ellenberg nitrogen difference maximum-minimum
v139	R.min	Ellenberg pH minimum
v140	R.max	Ellenberg pH maximum
v141	R.med	Ellenberg pH median
v142	R.maxmin	Ellenberg pH difference maximum-minimum
v143	S.min	Ellenberg salinity minimum
v144	S.max	Ellenberg salinity maximum
v145	S.med	Ellenberg salinity median
v146	S.maxmin	Ellenberg salinity difference maximum-minimum

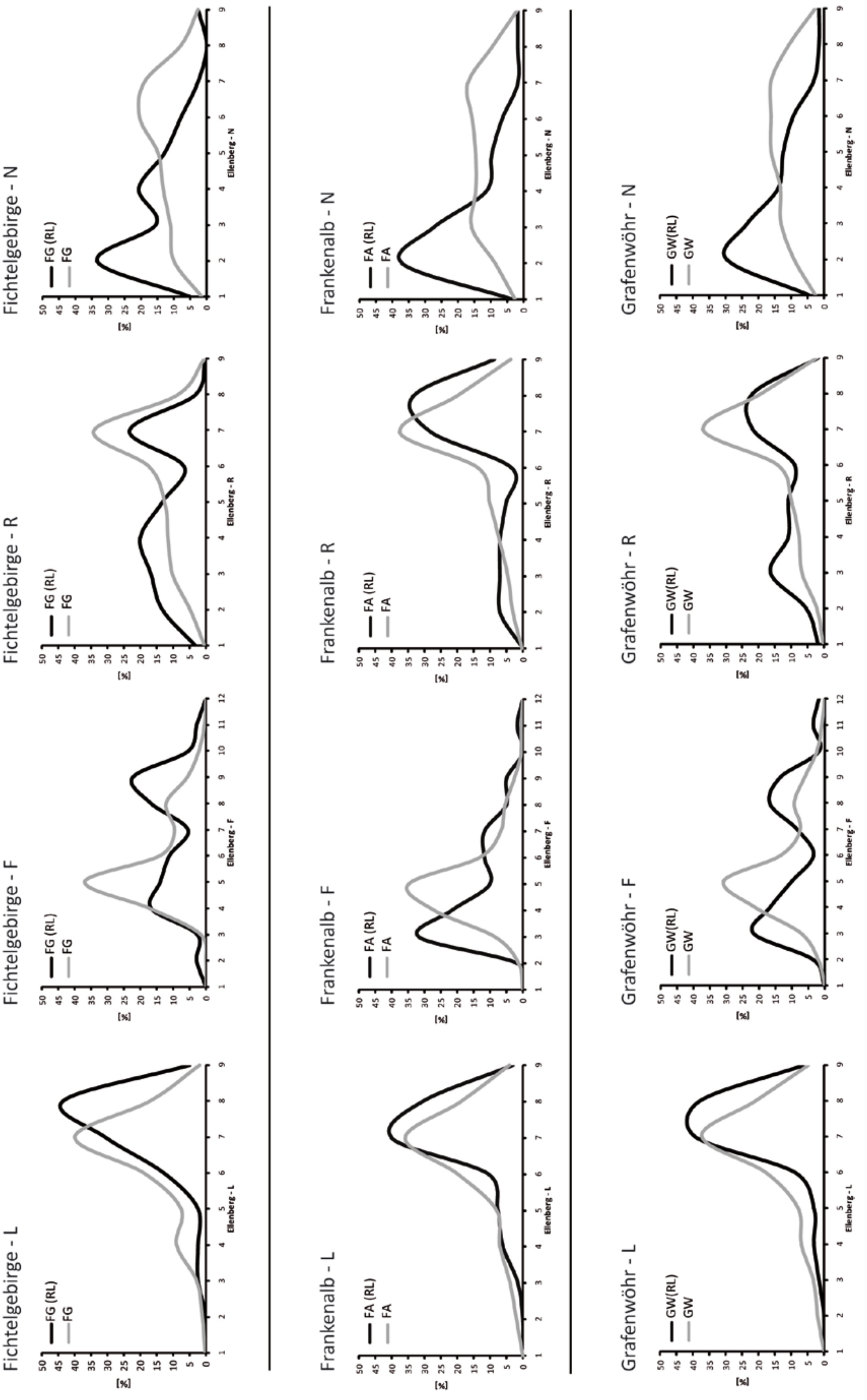
S 2: Red-listed species and their occurrence in combination with a certain land-use type.

Land-use type	**RL-1 (%)**	**RL-2 (%)**	**RL-3 (%)**	**RL-V/G (%)**	**total (%)**
fallow land/succession	100.0	32.4	32.2	39.6	38.5
grassland	0.0	20.0	8.0	22.6	21.2
forest	0.0	6.7	34.5	14.4	15.2
transition zone	0.0	16.2	10.3	10.2	10.8
path	0.0	18.1	1.1	6.4	7.1
water body	0.0	6.7	10.3	6.0	6.4
settlement	0.0	0.0	3.4	0.4	0.6
misc. constructions	0.0	0.0	0.0	0.3	0.3
rock	0.0	0.0	0.0	0.0	0.0

S 3: Red-listed species and their occurrence in combination with a certain disturbance type.

Disturbance type	**RL-1 (%)**	**RL-2 (%)**	**RL-3 (%)**	**RL-V/G (%)**	**total (%)**
compaction (wheels)	25.0	21.9	21.6	22.7	22.6
macroherbivory	25.0	7.5	17.7	15.8	15.2
compaction (tracks)	0.0	17.8	8.2	14.1	13.9
mowing	0.0	8.6	4.8	10.4	9.7
compaction (trampling)	25.0	8.9	8.7	9.1	9.1
foreign material	0.0	12.0	3.5	4.9	5.4
single tree felling	0.0	2.7	8.2	4.0	4.2
depression (water filled)	0.0	1.0	6.9	3.6	3.6
gravel (lime)	0.0	8.6	1.3	2.9	3.3
wildboar	0.0	2.1	3.5	2.4	2.4
hydraulic engineering	0.0	1.7	1.3	1.5	1.5
breakage	0.0	0.3	3.5	1.3	1.4
clear felling	25.0	0.3	2.6	1.3	1.3
fire	0.0	0.7	0.9	1.4	1.3
excavation (open)	0.0	1.7	0.0	1.3	1.3
grove felling	0.0	0.0	2.2	0.7	0.7
fencing	0.0	0.7	1.3	0.6	0.6
gravel (basalt)	0.0	0.0	0.0	0.4	0.3
seeding	0.0	1.4	0.9	0.1	0.3
skidding track	0.0	0.0	1.3	0.2	0.3
soil/rock movements	0.0	0.3	0.0	0.2	0.2
erosion (water)	0.0	0.0	0.0	0.2	0.2
biomass (export)	0.0	0.3	0.0	0.1	0.1
flooding	0.0	0.3	0.4	0.1	0.1
leveling	0.0	0.0	0.0	0.2	0.1
material storing	0.0	0.0	0.0	0.1	0.1
nutrient input	0.0	0.0	0.0	0.1	0.1
thinning	0.0	0.0	0.9	0.0	0.1
contamination	0.0	0.3	0.0	0.0	0.1
sealing	0.0	0.0	0.0	0.1	0.1
biomass (input)	0.0	0.3	0.0	0.0	0.0
creek reallocation	0.0	0.0	0.4	0.0	0.0
wood storage/movement	0.0	0.3	0.0	0.0	0.0
quarry	0.0	0.0	0.0	0.0	0.0
rejuvenation	0.0	0.0	0.0	0.0	0.0

S 4: Ellenberg indicator values of red-listed and common plant species.



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Education

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06/2009 - 03/2011	Scientific assistant at the Institute for Environmental Sciences, Geoecology & Physical Geography Group
01/2009 - 05/2009	Scientific assistant at the Bayreuth Center of Ecology and Environmental Research BAYCEER
01/2008 - 05/2009	Scientific assistant at the Disturbance Ecology and Vegetation Dynamics Group, University of Bayreuth
07/2007 - 12/2007	Scientific assistant at the Chair of Biogeography, University of Bayreuth
01/2007	Diploma in Geoecology, University of Bayreuth. Diploma thesis: *„Character and intensity of spatial and functional correlations between soil erosion/vegetation damage and grazing. The actual condition on the summer pastures in the Fergana Range, Southern Kyrgyzstan"*
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DECLARATION

Ich erkläre hiermit nach §8 der Promotionsordnung des Fachbereichs 7

- dass ich die eingereichte Dissertation selbstständig verfasst habe und alle von mir für die Arbeit benutzten Hilfsmittel und Quellen in der Arbeit angegeben sowie die Anteile etwaig beteiligter Mitarbeiterinnen oder Mitarbeiter sowie anderer Autorinnen oder Autoren klar gekennzeichnet sind;
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- dass mir bewusst ist, dass ein Verstoß gegen einen der vorgenannten Punkte den Entzug des Doktortitels bedeuten und ggf. auch weitere rechtliche Konsequenzen haben kann.

Landau, 15. September 2014

Martin Alt

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