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Homogenizing and diversifying effects of intensive agricultural land-use on plant species beta diversity in Central Europe — A call to adapt our conservation measures

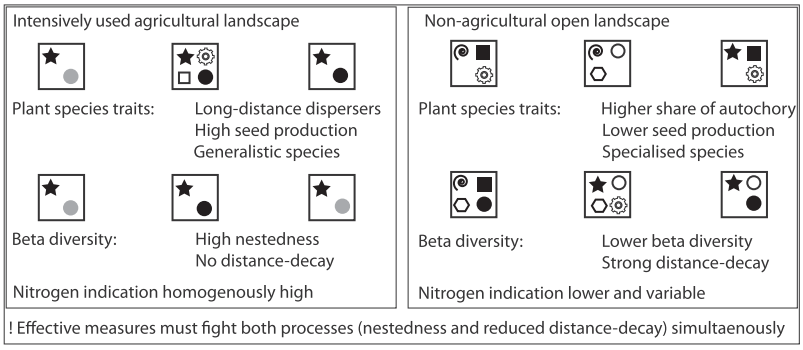
Constanze Buhk [a,*], Martin Alt [b], Manuel J. Steinbauer [c], Carl Beierkuhnlein [d], Steven D. Warren [e], Anke Jentsch [f]

[a] Geoecology/Physical Geography, Institute for Environmental Sciences Landau, University of Koblenz-Landau, Landau, Germany
[b] Environmental and Soil Chemistry, Institute for Environmental Sciences Landau, University of Koblenz-Landau, Landau, Germany
[c] Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, 8000 Aarhus, Denmark
[d] Biogeography, University of Bayreuth, Bayreuth, Germany
[e] US Forest Service, Rocky Mountain Research Station, Provoe, UT, USA
[f] Disturbance Ecology, University of Bayreuth, Bayreuth, Germany

HIGHLIGHTS

- Processes responsible for species loss under intense agriculture are specified.
- Plant species trait filtering lead to species nestedness and loss of distance decay.
- Processes were induced by selection for generalist species and good dispersers.
- N indicator values show eutrophication and homogenization under intense agriculture.
- Action to combat phytodiversity loss must address both processes simultaneously.

GRAPHICAL ABSTRACT



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ABSTRACT

The prevention of biodiversity loss in agricultural landscapes to protect ecosystem stability and functions is of major importance to stabilize overall diversity. Intense agriculture leads to a loss in species richness and homogenization of species pools, but the processes behind are poorly understood due to a lack of systematic case studies: The specific impacts by agriculture in contrast to other land-use creating open habitat are not studied as such landscapes hardly exist in temperate regions.

Applying systematic grids, we compared the plant species distribution at the landscape scale between an active military training areas in Europe and an adjacent rather intensively used agricultural landscape. As the study areas differ mainly in the type of disturbance regime (agricultural vs. non-agricultural), differences in species pattern can be traced back more or less directly to the management. Species trait analyses and multiple measures of beta diversity were applied to differentiate between species similarities between plots, distance-decay, or nestedness.

Contrary to our expectation, overall beta diversity in the agricultural area was not reduced but increased under agricultural. This was probably the result of species nestedness due to fragmentation. The natural process of

* Corresponding author.
E-mail addresses: buhk@uni-landau.de (C. Buhk), alt@uni-landau.de (M. Alt), Steinbauer@bios.au.dk (M.J. Steinbauer), carl.beierkuhnlein@uni-bayreuth.de (C. Beierkuhnlein), swarren02@fs.fed.us (S.D. Warren), anke.jentsch@uni-bayreuth.de (A. Jentsch).

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increasing dissimilarity with distance (distance-decay) was suppressed by intense agricultural land-use, generalist and long-distance dispersers gained importance, while rare species lost continuity.
There are two independent processes that need to be addressed separately to halt biodiversity loss in agricultural land. There is a need to conserve semi-natural open habitat patches of diverse size to favor poor dispersers and specialist species. At the same time, we stress the importance of mediating biotic homogenization caused by the decrease of distance-decay: The spread of long-distance dispersers in agricultural fields may be acceptable, however, optimized fertilizer input and erosion control are needed to stop the homogenization of environmental gradients due to nitrogen input into semi-natural habitat.

1. Introduction

Halting biodiversity loss is a central goal of world-wide conservation efforts (Convention on Biological Diversity, 2010) and is incorporated into European legislation within the Biodiversity Strategy to 2020 (European Commission, 2011). Over 45% of the European landscape is under agricultural use creating considerable need to protect species richness in cultural landscapes to halt overall biodiversity loss (Kleijn et al., 2011; Tscharntke et al., 2005). Land-use intensification has been found to be a major driver of the loss of biodiversity (Clavel et al., 2011; Foley, 2005; Sala et al., 2000) and ecosystem functions (Allan et al., 2015; Isbell et al., 2011; Isbell et al., 2013; Isbell et al., 2015; Rader et al., 2014). However, land-use intensification seems necessary to sustain food production for the increasing global human population (Tilman et al., 2011; Tscharntke et al., 2012a). What will a semi-intensively or intensively managed landscape look like if phytodiversity is to be conserved? Under intensive agricultural use, homogenizing effects on functional, taxonomic and genetic diversity occur (Olden et al., 2004) and are accompanied with habitat loss for specialised species (Foley, 2005; Meyer et al., 2013). Due to a lack of systematic studies linking species composition, pattern and trait analyses at the within-landscape scale, there is a large uncertainty regarding the processed responsible for species loss and reductions in diversity.

Phytodiversity of a landscape (gamma diversity) is strongly dependent on the extent of change in species composition between different land-use patches (beta diversity) within the landscape (Jurasinski et al., 2009; Tscharntke et al., 2012b; Whittaker, 1972). On the one hand, such dissimilarity in species composition between land-use patches is typically high in heterogeneous landscapes and decreases if the landscape is homogenized and simplified as under intense agricultural use (Benton et al., 2003; Gámez-Virués et al., 2015). On the other hand, dissimilarity in species composition between single land-use patches is also known to increase with rising geographical distance of the samples to each other (distance-decay effects; Nekola and White, 1999; Soininen et al., 2007). Distance-decay of species composition exists because larger similarity of environmental conditions tends to exist in closer vicinity than when located further away, thus affecting species sorting according to their particular niches. Secondly, distance-decay in species composition occurs because species dispersal potential declines considerably with greater distance. This is either due to dispersal barriers like forest patches that limit dispersal or due to neutral processes based on lower propagule pressure at larger distances than in nearby areas (Soininen et al., 2007). Intensive agricultural land-use might affect both factors negatively (reducing both environmental gradients and dispersal limitations) and might, thereby, lead to a decrease in distance-decay as compared to other landscapes. First, environmental gradients may weaken or disappear because intense agricultural land-use creates relatively large patches of homogenously treated land (fertilized, ploughed, treated with pesticides). This homogenization of environmental conditions favors generalist species with a wide physiological amplitude. These are mostly ruderal species that are able to live and reproduce successfully under various environmental conditions (Ekroos et al., 2010) making environmental gradients less important for species sorting processes (Clavel et al., 2011). Secondly, the reduction of dispersal limitations may happen because dispersal barriers like hedges disappear from the intensively used landscape (Benton et al., 2003; Ekroos et al., 2010). Furthermore, intense agricultural disturbance may select for species capable of long-distance dispersal. Species with effective long distance dispersal may quickly re-establish on intensively managed land from distant seed sources after heavy disturbance. In contrast, poor dispersers may suffer from fragmentation under intense agricultural land-use, as they survive only in remaining habitat fragments or disappear altogether (Ekroos et al., 2010; Gámez-Virués et al., 2015). Accordingly, specialist species (with narrow physiological niche width) that have low dispersal capacity – usually rare species - are disappearing from the landscape or suffer from fragmentation while strong dispersers as most generalist species become omnipresent (Henle et al., 2004; Meyer et al., 2013; Ozinga et al., 2005; Schweiger et al., 2005).

The process by which plant communities become more and more similar within larger areas is known as biotic homogenization (Olden and Rooney, 2006), and may be coupled with a decline in ecosystem functions and services (Clavel et al., 2011; Rader et al., 2014; Tscharntke et al., 2012a).

Previous work demonstrated higher similarity of plant communities or biotic homogenization between areas dominated by very strong land-use intensity over large distances across Europe (Dormann et al., 2007). For grasslands, a homogenizing trend, mainly due to high nitrogen input, has been demonstrated over Central Europe (Wesche et al., 2012) and within Switzerland (Bühler and Roth, 2011). However, the homogenizing role of semi-intense or intense agricultural land-use within open landscapes has never been compared with non-agricultural open landscapes. This may be because Central European landscapes tend to be realty affected by agricultural land-use and it is difficult to find adjacent landscapes that differ significantly in their disturbance regime (agricultural versus non-agricultural) but not in other fundamental characteristics.

Some existing studies indirectly approached the problem by sampling land-use intensity gradients (Kleyer, 1999; Meyer et al., 2013). In contrast, the present study directly utilizes the potential provided by one of the largest military training areas in Europe, thus enabling the comparison of adjacent open landscapes with very similar environmental characteristics but entirely differing disturbance regime and history. In addition, our study includes the monitoring of complete plant species identities on 1 ha plots which is larger than the size of typical land-use patches. Though this was very time consuming, it makes our dataset unique, as it allows not only differences between patches, but also landscape sections. Measures of beta diversity are explained according to species trait analyses at the within-landscape scale:

Our objectives are to disentangle processes of biotic homogenization, fragmentation and species distance-decay in similarity under the influence of agricultural land-use. The species trait analyses provide evidence sufficient to analyze if long-distance dispersers, generalists and nitrogen indicators are promoted under agricultural land-use as compared to non-agricultural use (military management coupled with semi-natural disturbances) and how this reflects the spatial patterns of species occurrence in the landscape. The understanding of the processes leading to species sorting and species loss are crucial to evaluate

and develop effective strategies to halt biodiversity loss in intensively used agricultural landscapes.

2. Materials and methods

2.1. Study area

The agricultural sample site consists of forest (about 40%), agriculture (38%), and grassland (22%) and is situated within the Fichtelgebirge in north-eastern Bavaria (32U 709860E, 5557570N), Germany. It covers an area of 16 km^2 and is located at an elevation of about 600 m. The geology of the area consists of granite to phyllite bedrock covered by acidic sandy to loamy, dystric Cambisols (Behrens et al., 1995; European Soil Bureau Network, 2005). Annual solar radiation varies from 1045 to 1104 kwh/m^2 and the sun shines about 1450–1599 h per year (Bayerische Staatsregierung, 2016). Precipitation averages 650 mm $year^{-1}$. Mean annual temperature is 7.3 °C (climate station Braunersgrün; Kerscher, 2009). Forestry manages mainly spruce plantations (*Picea abies*) and some beech forests (*Fagus sylvatica*), agriculture is dominated by cereal and corn production, and hay and silage is produced at mostly fertilized meadows of Arrhenatherion plant communities (a characteristic species is *Arrhenatherum elatius*). The landscape in the Fichtelgebirge is semi-intensively used but not yet completely homogenous in its structure as found in high intensity farming systems which makes it especially comparable to the training area.

The second study area is very similar in its structure, openness and disturbance intensity but the type of disturbance regime developed different for the last decades: The sample site used for comparison is a military training area located 48 km South of the first site (32U 694000E, 5508300N) with mostly similar abiotic characteristics: Plots were also sampled within an area of 16 km^2 between 440 and 560 m. The western third of the training area, where the study area is located is characterized by calcareous soils derived from Jurassic limestone sediments (Dill et al., 2009; Warren and Büttner, 2008) building haplic Luvisols or eutric Podsoluvisols (Behrens et al., 1995; European Soil Bureau Network, 2005). Annual solar radiation varies from 1060 to 1119 kwh/m^2 and the sun shines about 1500–1649 h per year (Bayerische Staatsregierung, 2016). The mean annual temperature is 7.5 °C and the annual precipitation is 700 mm $year^{-1}$ (climate station Eschenbach, German Weather Service). The site is managed as a semi-natural state with annual mowing of grasslands (Arrhenatherion plant communities) and some forestry management (mainly spruce, beech and pines). Macroherbivores like deer and wild boar are abundant. The area is characterized by grassland (38%), forest (about 35%), and fallow land (about 20%). The dominating land-use since 1910 until today is military training, which includes the use of tanks, military maneuvers and excavation activities (Warren and Büttner, 2008).

The main abiotic difference between the areas is the geological substrate and subsequently the soil type. As they are evenly spread over the area and both soils are of minor quality this may partly influence species pools leading to more calciferous plants (Chytrý et al., 2003) in the military training area but there is no indication that pattern of species richness are influenced.

2.2. Sampling design

A regular grid of 100 quadratic plots was established for both study sites (compare Buhk et al., 2007; Fig. 1a, b). For the plot-based analysis on hand, forest plots (of over 25% of forest) were excluded, as the focus of the study refers to open landscape patches only. 53 plots within the agricultural area and 66 plots within the military training area could be used for analysis. The plots had a distance of 400 m between each center with a grain size of 1 ha (100 m × 100 m) each, which allows the inclusion of several land-use patches within each plot in open habitat. Within each plot, all patches of different land-use or disturbance regimes were characterized that had a minimal size of 10 m^2 including footpaths and transition patches of >1 m in width (see Buhk et al., 2007). As an example, a plot may include 5 patches: a section of a road including narrow road margins, an agricultural field, a field margin, a piece of a meadow and a track. Within each patch, a complete list of vascular plant species was recorded (presence/absence data). For the diversity measures, species lists per plot were used. For the analyses of species traits for all patches within the selected open habitat plots, the median of all selected traits was calculated and averaged to the plot level. In this way, a "weighted" average could be built though the species data is presence/absence data, only. There were 341 patches included in the trait analyses from the agricultural area and 421 patches in the military training area.

2.3. Species trait analyses

To characterize effective and long-distance dispersal ability of species, trait data on "mean seed numbers" and "dispersal strategy" was extracted from the Leda Traitbase (Kleyer et al., 2008) and "mean seed weight" and "reproduction type" from BIOLFLOR (Klotz et al., 2002). To differentiate generalist species from specialist species, data on the "number of biotope types" typically colonized (extracted from BIOLFLOR), were used to estimate the "width of niche" of the species. As many species use several dispersal strategies, an index of importance for, each specific type was calculated. For each species a maximum of four credits was divided between the four major dispersal types: autochory, hemerochory, anemochory and zoochory. A species using anemochory and zoochory, for example, received two credits for each of the two dispersal types. A species using anemochory only, received four credits in anemochory (similar to Burmeier et al., 2010). For reproduction type, three credits were divided between the 2 characteristics. As an example, mainly seeding behavior but some vegetative growth (ssv) was characterizes by 2 credits for the seeding and 1 credit for the vegetative reproductive growth while similar strength of both characteristics was reproduced as 1.5 credits each. Trait information was not available for all species. In the agricultural area, trait information on 368 species (number of biotope types), 343 species (dispersal strategy), 255 species (reproduction type), 314 species (mean seed number), and 299 species (seed weight) were included into the analyses. In the military training area 541 species (number of biotope types), 510 species (dispersal strategy), 376 species (reproduction type), 453 species (mean seed number) and 456 species (seed weight) were analyzed. As generalist and nutrient-loving species are often neophytic plant species (Clavel et al., 2011), the median number of neophytes in the patches per plot was calculated and compared. As trait composition may be directly linked to nutrient enrichment, the Ellenberg indicator value N was added as a surrogate variable to the analyses (Ellenberg, 2001).

2.4. Statistical analyses

Species numbers per plot were calculated from the patch based sampling data, as were numbers of rare species per plot. A species was declared as "rare" if listed in the Bavarian red list either as protected (RL 1–3) or classified in the early warning list (RL G/V; STMUG, 2005).

Measures of beta diversity are manifold and their applicability and usefulness is under ongoing debate (Anderson et al., 2011; Baselga, 2010, 2012, 2013; Chao et al., 2005; Jurasinski et al., 2009; Koleff et al., 2003; Legendre et al., 2008; Legendre et al., 2013; Legendre, 2014; Morlon et al., 2008; Podani and Schmera, 2011; Tuomisto, 2010; Tuomisto and Ruokolainen, 2006, 2008). Acknowledging the current state of the discussion, we applied gradient and non-gradient analyses of species dissimilarity (according to Vellend, 2001 and decided to use the following measures to characterize beta diversity)

a) To analyze if overall species richness (gamma diversity) in the two areas is increased due to overall high alpha diversity in the single plots or mainly due to strong differences in species composition

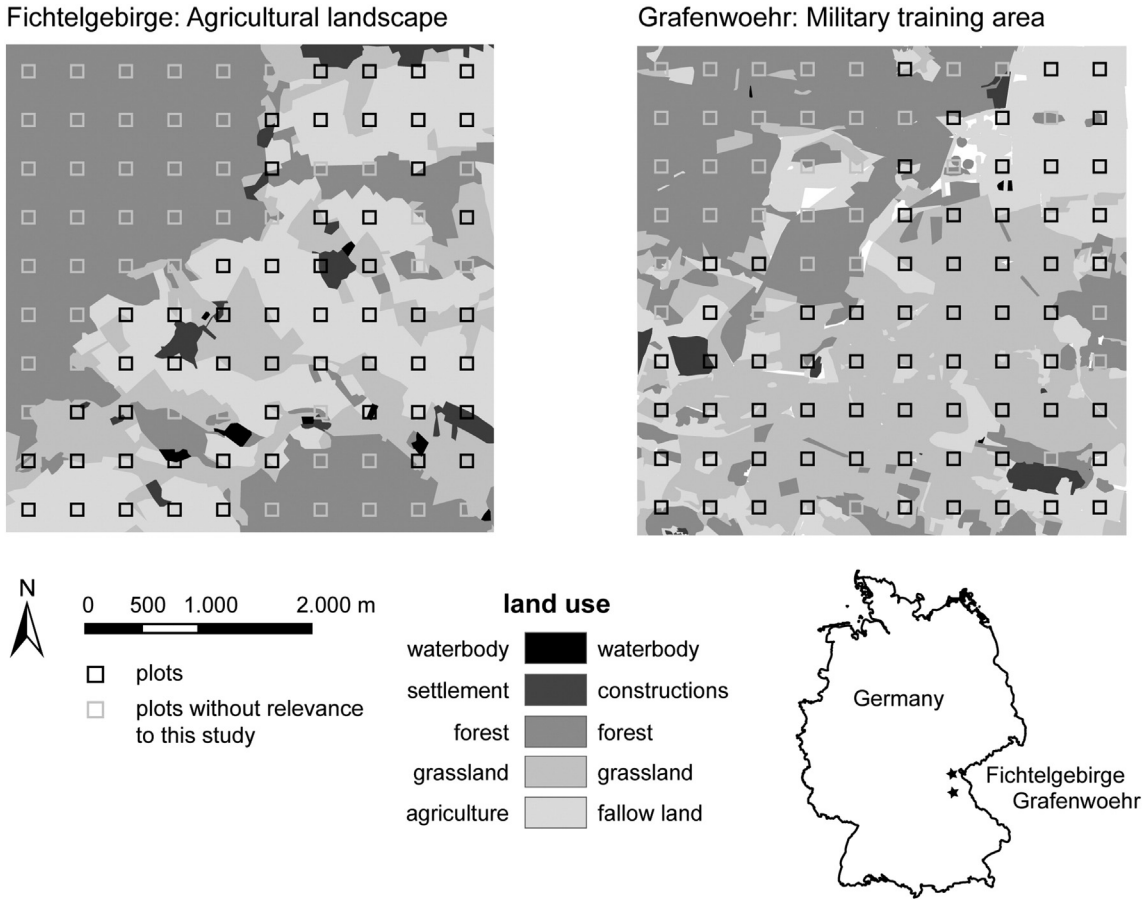

Fig. 1. Location of the agricultural landscape (Fichtelgebirge; left) and the military training area (Grafenwoehr; right). Study design: a systematic grid was laid over an area of 4 × 4 km. Each plot comprises an area of 100 m × 100 m. Within each plot vascular plant species presence/absence data were recorded. For this study on hand, solely plots of <25% forest cover were included (black squares). Forest plots were not of relevance within this study (grey squares).

between plots, the well-known and often used index "additive partitioning" (Veech et al., 2002), "Whittaker's effective species turnover" (Tuomisto, 2010) or "proportional diversity" (Jurasinski et al., 2009) was used. The Index relates the overall species richness (γ; gamma diversity) to the mean species richness of the plots ($\overline{\alpha}$; alpha) (Koleff et al., 2003; Tuomisto, 2010; Vellend, 2001). The larger the value, the more different are the plots from each other in terms of species composition; the smaller the value, the higher the importance of single plot richness for gamma diversity.

b) As a similarity measure for pairs of samples, we applied the widely used and accepted Simpson's similarity Index. This measure satisfies the criteria of linearity, homogeneity (if all values are multiplied by the same factor, the value does not change), symmetry, scaling between 0 and 1, and is not strongly affected by overall differences in species richness between the sample groups (Koleff et al., 2003; Legendre, 2014). To compare the pair-wise Simpson similarities between the two landscapes, the method of multivariate dispersion as characterized by Anderson et al. (2006) was used.

c) In order to measure species turnover in a narrower sense or distance-decay (see Jurasinski et al., 2009) between the plots along geographic distance, linear regression analyses were used. Pair-wise similarity of species composition in the plots (Simpson similarity) was explained via the corresponding geographical sample distances. As proposed by Nekola and White (1999), we also plotted log transformed species similarity versus distance for comparison, and fitted linear regression models. The results did not differ strongly, thus only the untransformed data are presented (compare to Tuomisto, 2010). The significance of the results was assessed using Mantel tests with 1000 permutations (Legendre and Legendre, 2012).

d) Finally, a multiple site similarity measure was applied to distinguish between species richness effects, species turnover and species nestedness over the whole set of samples for each landscape which is an alternative measure to averaging pair-wise similarities of samples (Baselga, 2010). Several indices exist (Baselga, 2013; Carvalheiro et al., 2013). We decided to use the recently proposed Jaccard based measures $beta_{CC}$ indicating overall beta diversity which is the sum of the real turnover component $beta_{3M}$ and the richness component $beta_{RICH}$ which signalizes nestedness (Ensing and Pither, 2015).

The procedures were carried out using R 3.1.3 (R Core Team, 2015) with the package vegan 2.2-1 (Oksanen et al., 2015) for similarity analyses, plus the packages simba (Jurasinski and Retzer, 2012) and ecodist (Goslee et al., 2007). Multiple beta similarity measures were calculated according to the R script presented in Ensing and Pither (2015).

The importance of each trait per plot in the two areas was compared using Mann-Whitney-U tests. The single values for each plot were derived from the median of all values per patch in the plot. For trait data analyses, SPSS 23 (IBM SPSS Statistics Version 23.0.0, 2015) was used.

3. Results

Diversity measures calculated are summarized in Table 1. While overall species richness is clearly higher in the military training area, the average percentage of rare species from overall richness was about 9% in both landscapes. There is an average of 3% of rare species in the plots in the agricultural area versus 4% in the military training area.

Table 1
Diversity measures calculated in the open landscape plots in the agricultural landscape and in the military training area. CI stands for confidence interval. Further explanation and statistics of the multivariate dispersal measure and the distance-decay measure are presented in the text.

Diversity measure	Agricultural landscape	Military training area
Total species numbers	378	553
Mean spec. numbers per plot	71 (±8 CI)	140 (±8.16 CI)
Total protected spec. numbers	35	50
Mean protected spec. numbers	2.2 (±0.8 CI)	5.6 (±0.6 CI)
Whittakers's effective turnover	4.32	2.95
Simpson dissimilarity (distance to median in multivar. dispersion)	0.23	0.2
Distance-decay of Simpson similarity	Slope: −7e−06 Adj. R^2: 0.002, n.s.	Slope: −1.9e−05 Adj. R^2: 0.035, $p < 0.001$
$Beta_{CC}$	0.966	0.965
$Beta_{3M}$	0.498	0.634
$Beta_{RICH}$	0.468	0.331

However, this apparent similarity in numbers is misleading, as the distribution of rare species in the agricultural area is very heterogeneous while it is very homogenous in the military training area: Only two plots in the agricultural area were inhabited by >5 protected species. In one third of the plots, not a single protected species was found. In the military training area, in contrast, roughly half of the plots were inhabited by >5 protected species and no plot was bare of any protected species.

Whittaker's effective species turnover was clearly higher in the agricultural landscape versus the military training area (Table 1). Multivariate dispersion indicates a similar trend towards higher pair-wise Simpson dissimilarity between plots in the agricultural area (Table 1). This smaller difference is marginally significant according to the permutation based ANOVA with $F = 3.77$ and $p = 0.0547$. Fig. 2 shows that similarities in the agricultural landscape tend to be either very low (very long vectors towards the median) or very large (short vectors) while we find predominately low to intermediate distances or large to intermediate similarities in the military training area.

The linear regression analysis combining species similarity with distance (turnover according to Jurasinski et al., 2009) revealed that the regression coefficient value for the agricultural area was not significant, indicating no distance-decay, while distance-decay was found in the military training area (slope: −1.9e−05; adjusted R^2 of 0.035***; Fig. 3).

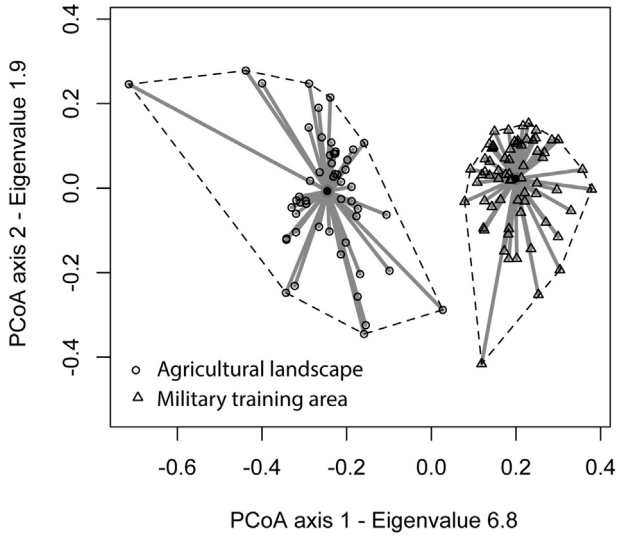

Fig. 2. Graphical presentation of distances to median in multivariate dispersion basing on Simpson similarity measures. Grey lines indicate the distances of each pair-wise similarity measure to the multivariate median separately for both landscapes.

The multiple similarity measures including not only pair-wise samples of similarity but considering all plots simultaneously reveal similar overall multiple-site dissimilarity $beta_{CC}$ in the landscapes (Table 1). In contrast, the replacement component or real species turnover measured as $beta_{3M}$ is clearly smaller in the agricultural area as compared to the military area. For the nestedness-resultant multiple-site dissimilarity $beta_{RICH}$ the opposite is found (Table 1).

Species trait analyses reveal several significant differences in trait distribution between the two landscapes (Table 2). In the intensively used agricultural landscape species that set high numbers of lightweight seeds are more common than in the military training area. The importance of anemochorous dispersal strategy quadruples while autochory is clearly less important as compared to the military training area. Seeders became more relevant in the agricultural landscape though the seeding strategy remains the most important form of reproduction in the military training area also.

Species inhabiting more habitat types were significantly overrepresented in the intensively used agricultural landscape as compared to the military training area though the magnitude of the difference is not large (Table 2). The median number of different neophyte species per patch is similarly low in both areas. While most findings in the agricultural area are two distinct species (*Matricaria discoidea* and *Lolium multiflorum*) there is a higher variety of species of lower consistency in the military training area mainly found along roads. The Ellenberg indicator values for N are higher in the agricultural area but the standard deviation is clearly higher in the military training area which indicates large differences of nitrogen availability between the plots in the military area versus similar high levels of nitrogen availability under intense agricultural use (Table 2).

4. Discussion

Comparing effects of agricultural land-use with adjacent open habitat of different management revealed contrasting results concerning different measures of beta diversity at the landscape scale: While agricultural land-use lead to a diversifying effects with higher pair-wise Simpson beta diversity and Whittaker's beta diversity measure, multiple similarity measures revealed no difference between the landscapes but the phenomenon of distance-decay was suppressed under agricultural land-use having a homogenizing effect with distance.

4.1. Agricultural land-use reduces distance-decay

Soininen et al. (2007) found distance-decay to be ubiquitous at various scales and for many organism groups and ecosystems. However, most distance-decay studies focus on semi-natural or pristine habitats. In intensively used agricultural landscapes, natural processes like environmental gradients and dispersal limits may be super-imposed by agricultural land-use (Buhk et al., 2007). The slope for the linear distance-decay in Simpson similarity found in the military training area is rather steep in comparison with the literature (Soininen et al., 2007; Steinbauer et al., 2012) but in accordance with distance-decay studies at the same scale (Girdler and Connor Barrie, 2008; Jones et al., 2006). Consequently, high distance-decay is present in the military training area, while it is not found at similar distances in the studied agricultural area. The factors that are influencing the intensity of distance-decay were found to be strongly scale-dependent (Condit, 2002) and sensitive to grain and extent of a study (Keil et al., 2012; Steinbauer et al., 2012). As the study provides a comparison based on similar scale, open habitat type, group of species and latitude, the detected difference in distance-decay must truly depend on the type of human impact and is probably not strongly affected by other influences. What may be the causes for this homogenizing impact over distance? As expected, agricultural

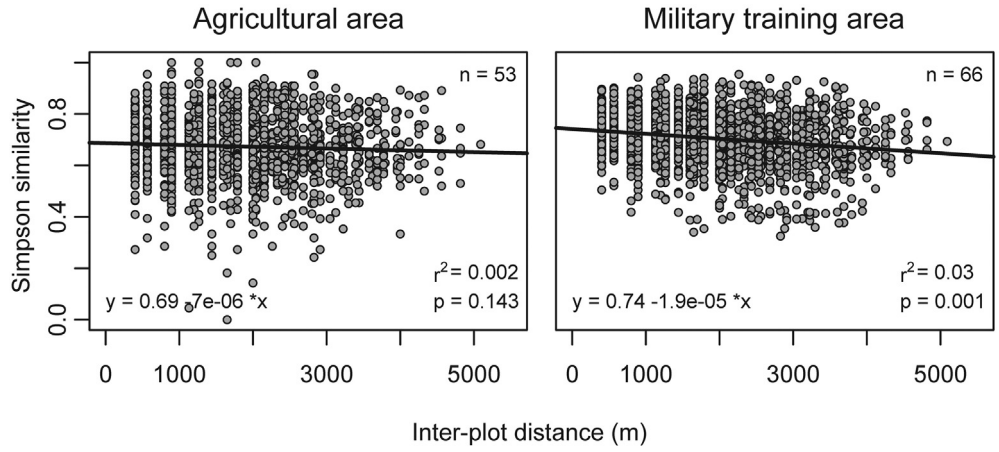

Fig. 3. Simpson similarity plotted against geographical distance reveals that no significant distance-decay is found in the agricultural landscape (left) while it is clearly verifiable in the military training area.

land-use might have affected both drivers of distance-decay (dispersal limitations and environmental gradients) negatively. Naturally, vascular plants show seed dispersal limitation even at smaller scales compared to the spatial extent and resolution of our study (Bin et al., 2010), however, the species found in the agricultural landscape show higher dispersal capacity as compared to species in the military training area. Long distance dispersers exhibit less distance-decay as compared to short distance dispersers. For example, at a landscape scale, Pteridophyta are known to exhibit less distance-decay than Spermatophyta due to their especially high dispersal capacity (Qian, 2009). In our work, at within-landscape scales, we find that effective dispersal of plants selected by agricultural land-use (mainly effectively wind dispersed seeders with lightweight seeds) possibly suppresses the pattern of distance-decay. We expect that agricultural land-use acted like a trait filter favoring long distance dispersers thereby reducing the decline in community similarity with distance, while this selection is missing in the military training area. Further, our data show that the plant species in the agricultural area are not just good dispersers but also generalists with wide euryoecious amplitude and indicators of high nutrient supply. This is supported by the number of habitat types inhabited (Buchi and Vuilleumier, 2014) and elevated Ellenberg N indicator values and makes environmental gradients that could also lead to distance-decay irrelevant. As the Ellenberg indicator N values are higher and less variable in the agricultural landscape as compared to the military area we can assume that environmental conditions have been homogenized at a high nutrient level throughout the area (Smart et al., 2003) which reduces environmental gradients and consecutively also distance-decay. The selection for certain species traits is a typical phenomenon of biotic homogenization with a few winners of similar trait combinations and wide ecological niche (Bühler and Roth, 2011; Gámez-Virués et al., 2015; Olden and Rooney, 2006; Smart et al., 2005). We emphasize that the species selection towards generalists and strong distance dispersers is not just a matter of habitat disturbance per se. Both, the military training area and the agricultural area present a wide variety of different kinds of disturbances, both are heavily disturbed areas (Alt, 2015; Buhk et al., 2007). Military training landscapes in general will exhibit a wider range of disturbance kinds and intensities than will agricultural landscapes. The objective of agriculture is generally to homogenize the landscape in order to have areas of uniformly high productivity. Military landscapes have no such objective. Uniformity of disturbance is created only when the landscape has uniform military benefit. Such is seldom the case. Military value is determined by many factors related to such things as smoothness of terrain, access to military targets or objectives, proximity to perceived traffic or targeting obstructions, nearness of military objectives, refueling areas, supply provisioning areas, etc. The differences in disturbance regimes were analyzed: The overall number of disturbance types is higher in the military training area (35) than in the agricultural area (21), with 15 disturbance types shared between both study sites. Only three disturbance types, agricultural use/ploughing (38.8%), compaction of soil by wheeled vehicles (27.7%), and mowing (26.9%), cover over 90% of the agricultural area and most disturbances do not overlap. In contrast, many more disturbance types are prominent in the military training area and disturbances tend to be nested in each other for example with small scale disturbances by deer within a matrix of a meadow mown once a year or single tracks of military vehicles or men in fallow land. The spatially

Table 2
Analyses of plant species trait characteristics in the agricultural landscapes and in the military training area. Calculated means and their lower and upper limit of the 95% confidence interval are given to see the quantity and direction of change. Higher values are written in bold, if the differences were significant (according to Mann-Whitney U Tests). Means of the plots were calculated on the basis of the information collected in the patches. For seed numbers and seed weight the average per plot was calculated. For the other parameters, the median of the single patches was used.

	Agricultural landscape Mean (95% CI limits)	Military training area Mean (95% CI limits)	Mann–Whitney U	p
Average seed numbers	**5423 (4856/5990)**	3229 (2929/3529)	544	<0.001
Average seed weight [mg]	1.05 (0.92/1.17)	**1.21 (1.14/1.27)**	2454	<0.001
Importance of anemochory	**0.52 (0.45/0.6)**	0.13 (0.09/0.18)	471	<0.001
Importance of autochory	0.5 (0.43/0.57)	**0.9 (0.86/0.93)**	3218	<0.001
Importance of hemerochory	1.33 (1.32/1.35)	1.33 (1.33/1.33)	1903	0.31
Importance of zoochory	**1.36 (1.34/1.38)**	1.33 (1.33/1.33)	1386	0.008
Reproduction type seeds	**2.25 (2.14/2.35)**	1.92 (1.89/1.95)	762	<0.001
Number of habitats types	**3.96 (3.9/4.03)**	3.85 (3.81/3.89)	1237	0.006
Number of neophytes	0.59 (0.42/0.75)	0.57 (0.38/0.75)	1634	0.51
Ellenberg indicator N	**6.02 (5.92/6.12)**	5.08 (4.98/5.18)	292	<0.001
St.Dev Ellenberg N	1.62 (1.56/1.68)	**1.7 (1.7/1.74)**	2290	0.004

more heterogeneous disturbance pattern in the training area favors a larger variety of traits in the species pool. This links to the strong relationship between disturbance regime heterogeneity and species richness (Buhk et al., 2007; Jentsch et al., 2012; Warren et al., 2007). In addition, there are some very specific effects of military disturbances that have to be taken into account when comparing the pattern found, that is very strong local disturbance at explosion sites or tank maneuver sites. Explosion sites are not located in the study area. They are located further East. Concerning the tank maneuvers, data indicate that such punctual effects are of minor importance concerning our analyses of the distance decay effect as calculated here between the plots: areas of completely distinct species compositions was found on patch scale but not on plot scale in the analyses. The training area, in contrast, shows relatively high homogeneity of very species rich plots that slowly change species composition with increasing distance (distance decay effect).

4.2. Partitioning of beta diversity measures

Whittaker's effective turnover is clearly higher in the agricultural landscape as compared to the military training area which shows that the difference of the species composition between the plots in the agricultural area contributes more to overall gamma diversity (species numbers at landscape scale) than the species numbers in the single plots. The pair-wise analysis using the Simpson diversity measure confirms this larger difference in species composition between the plots in the agricultural landscape than in the military area. However, beta diversity measures considering the whole species pool when comparing plot similarities do not indicate a larger dissimilarity under agricultural use. This is, because the major part of the species in the rather intensively used plots in the agricultural landscape is just a subset of the species from the richer plots which may be also called nested: in the agricultural landscape a few plots exist with a reasonable number of species while many other plots give home to only a few species which are a small subset of the species rich plots (Baselga, 2010). There is a non–compensatory loss of species between plots which is responsible for the differentiation of the communities under agricultural and it is indicated by the higher degree of nestedness (compare to Villegas Vallejos et al., 2016). Our initial statement from the introduction that landscape richness is especially dependent on beta diversity between plots is obviously not true, here. Mean species numbers at the 1 ha plot scale (alpha diversity) were about 50% less in the agricultural area while species numbers at the landscape scale (gamma diversity) were only about 30% less. This difference in the species reduction depending on scale goes well along with the lower measured between plot Simpson similarities (higher beta diversity) in the agricultural area as compared to the military training area because species are more equally distributed within the military area and even protected species occur regularly keeping plots similar. The percentage of rare species was astonishingly high even in the intensively used agricultural area with 9% at landscape scale but only 3% at plot scale (in the military area: 4% at plot scale). On the one hand, we have a poorer species pool in the agricultural area as compared to the military area especially at the plot scale and fragmented habitat for rare species. On the other hand, rare species are not that rare in the military area but are omnipresent though a clear turnover of species between plots (see low percentage of protected species at plot scale). The missing rarity of "rare species" in the military training area is not a contradiction as "rare species" was defined as being protected for its rarity in Bavaria and species may locally still be abundant. Differences in bedrock cannot explain the much poorer species pool of the agricultural area as compared to the military area. Regionally, the calcareous bedrock of the military training area may have an about 4% larger species pool as compared to the siliceous bedrock in the agricultural area (Chytrý et al., 2003). This is far from explaining the large differences found. We therefore assume that a major part of the species was already lost from the agricultural landscape due to the type of management and the few remaining species rich plots are fundamental for the conservation of the present diversity.

Apart from the influence of the management leading to certain disturbance regimes, there is also a local anthropogenic influence on abiotic factors probably bringing some diversity into the system. In both landscapes there is road and path gravel from outside the area that influence local diversity due to altered mineral composition and soil pH. In the agricultural landscape the influence of liming of the fish ponds had a diversifying influence on the local plant composition (unpublished data). Another foreign material that changes the abiotic conditions in the agricultural landscape is the locally intensive use of fertilizers: Generalists as well as nitrogen loving ruderal species clearly gained importance under intense agricultural use, indicating the loss of primarily species with lower N-Ellenberg indicator values and short distance dispersal – probably specialist species. The agricultural land-use leads to habitat fragmentation for the remaining specialist species (Buchi and Vuilleumier, 2014; Clavel et al., 2011).

4.3. Species conservation in intensely used agricultural landscapes

With our data we can separate 2 distinct processes that may have to be addressed independently by conservation actions. First, there is homogenization over geographical distances even at the within landscape scale reducing distance-decay due the species filtering for good dispersers and generalists and due to a reduction of environmental gradients due to the overall eutrophication of the landscape. Second, there is an enhanced dissimilarity of plots under agriculture as a result of the nestedness of the species: a few plots are inhabited by a large set of species while the others give home to only small subsets of the species found in the fragmented habitat remnants. These processes probably occur in all intensively used agricultural areas (Dormann et al., 2007) within the temperate zone, as modern agricultural practices (such as high nutrient supply, soil disturbances like ploughing, compaction of the soil, herbicide pressure, openness of the landscape favoring wind dispersal, lack of pollinators, …) are very similar throughout the ecozone and only few areas are still under traditional use (Sutcliffe et al., 2015). This leads to the dominance of plants with the same traits – usually also of close phylogenetic similarity (van Meerbeek et al., 2014; Winter et al., 2009).

Agro-environmental schemes widely applied throughout Europe mostly fight our second mentioned process: habitat loss for specialist species. With compensation payments to farmers, politicians try to conserve, re-establish and connect some of the fragmented habitats by using them in an extensive, traditional manner. Given that these measures are no "flat-rate payments" but are adapted to the respective landscape and situation, such actions recently have been found successful in halting regional biodiversity loss (Carvalheiro et al., 2013 but see Kleijn and Sutherland, 2003; Tscharntke et al., 2005).

In contrast, the first highlighted process describing reduced distance-decay and consecutively biotic homogenization seems more difficult to address. Omnipresent generalists and long distance dispersers in fields and field margins may not be a problem. They do not systematically out-compete other species but use short-term available niches to establish and reproduce themselves and may therefore not lead to an overall biodiversity loss. However, the reduction of environmental gradients that is mainly pushed by overall landscape eutrophication is a large problem because eutrophication does not stop at the borders of the fields (Vitousek et al., 2009) but affects the semi-natural landscape patches reducing the competitive ability of specialist species or species of minor affinity to nutrients (Zechmeister et al., 2003). Accordingly, agro-environmental schemes favoring specialists in habitat fragments would become ineffective if the process of biotic homogenization due to eutrophication would not be combated simultaneously. Modern agricultural techniques provide large potential to optimize nutrient input and reduce erosion by either wind or water (Chalk

et al., 2015; Florio et al., 2016; Panagos et al., 2015a; Shaviv and Mikkelsen, 1993; Tilman et al., 2002; Wang et al., 2015). Landscape eutrophication is not just caused by agriculture (Galloway et al., 2008) and also other nutrient sources will have to be reduced. However, if fragmented habitat patches are found within a matrix of intensely managed fields, the direct input from the matrix to the habitat remnant is most likely the largest source of nutrients.

With this work on hand we demonstrate the importance of conservation action in intensively used agricultural areas. Though intense agricultural production might be necessary in some areas to sustain food production, there is no need for overproduction in temperate regions to combat hunger elsewhere in the world as much of the food spoils instead of reaching needy people (Gomiero et al., 2011; Tscharntke et al., 2012a). Intensive agriculture has been found to be commonly unsustainable (Gomiero et al., 2011) especially in areas with hilly topography and easily erodible soil types as erosion threatens further productivity (Panagos et al., 2015b), and, as a feedback loop, intensification using even more mineral fertilizers will not contribute to further increase in productivity (Wiesmeier et al., 2015). Especially in regions with still existing extensive traditional land-sharing systems, conservation of the traditional management and high species richness should have priority for either intensification or abandonment (Müller et al., 2016; Stoate et al., 2009; Sutcliffe et al., 2015). It is much more difficult to recuperate diversity than to conserve it (Tscharntke et al., 2005). Over all, regional specific programs creating heterogeneous landscapes are needed (Buhk et al., 2007; Duflot et al., 2014; Ponisio et al., 2016; Rösch et al., 2015) and nutrient additions in intensively used patches must be optimized to reduce landscape eutrophication and biotic homogenization within and between landscape scales (Smart et al., 2003; Wesche et al., 2012).

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