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Towards the development of general rules describing landscape heterogeneity-multifunctionality relationships

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ABSTRACT

1. Rapid growth of the world's human population has increased pressure on landscapes to deliver high levels of multiple ecosystem services, including food and fibre production, carbon storage, biodiversity conservation and recreation. However, we currently lack general principles describing how to achieve this landscape multifunctionality.

2. We combine theoretical simulations and empirical data on 14 ecosystem services measured across 150 grasslands in three German regions. In doing so, we investigate the circumstances under which spatial heterogeneity in a driver of ecosystem functioning (an 'ecosystem-driver,' e.g. the presence of keystone species, land-use intensification or habitat types) increases landscape-level ecosystem multifunctionality.

3. Simulations based on theoretical data demonstrated that relationships between heterogeneity and landscape multifunctionality are highly variable and can range from non-significant to strongly positive. Despite this variability, we could identify criteria under which heterogeneity-landscape multifunctionality relationships were most strongly positive: this happened when multiple ecosystem services responded contrastingly (both positively and negatively) to an ecosystem-driver.

4. These findings were confirmed using empirical data, which showed that heterogeneity in land-use intensity promoted landscape multifunctionality in cases where

functions with both positive (e.g. plant biomass) and negative (e.g. flower cover) responses to land use intensification were included. For example, the simultaneous provisioning of ecosystem functions related to forage production (generally profiting from land-use intensification), biodiversity conservation and recreation (generally decreasing with land-use intensification) was highest in landscapes consisting of sites varying in land-use intensity.

5. *Synthesis and applications*. Our findings show that there are general principles governing landscape multifunctionality. A knowledge of these principles may support land management decisions. For example, knowledge of relationships between ecosystem services and their drivers, such as land use type, can help estimate the consequences of increasing or decreasing heterogeneity for landscape-level ecosystem service supply, although interactions between landscape units (e.g. the movement of pollinators) must also be considered.

KEY-WORDS: agricultural production, ecosystem multifunctionality, ecosystem services, grasslands, heterogeneity, landscape multifunctionality, land use intensity, trade-offs

INTRODUCTION

The world's population and its rate of resource consumption are growing rapidly (Steffen *et al.* 2015), placing increasing pressure on dwindling land resources to provide high and stable levels of multiple ecosystem services (ecosystem multifunctionality), including food, fibre and energy production, carbon storage, water purification, wildlife conservation and recreation (MEA, 2005). As a result, land-use conflicts are becoming increasingly common (Tilman *et al.* 2009; Goldstein *et al.* 2012). Management strategies minimizing these conflicts and promoting landscape-level multifunctionality are needed, but most research on this has focused on regional case studies (e.g. Chan *et al.* 2006; Qiu & Turner 2013). Therefore, we currently lack general principles to guide the management of multifunctional landscapes (Bennett *et al.* 2009).

In this study, we sought to describe general rules, applicable in a wide range of contexts, which determine the supply of multiple ecosystem services (multifunctionality) of landscapes. We also investigated if these rules can explain whether heterogeneity in land-use maximizes ecosystem multifunctionality. While other definitions are possible (Mastrangelo *et al.* 2014; Manning *et al.* 2018), we define a landscape as multifunctional when all desired ecosystem services are supplied at high levels in at least part of its area (van der Plas *et al.* 2016), and we define heterogeneity as a high spatial variation in a factor driving ecosystem services (e.g. habitat type or land-use intensity) among sites *within* a landscape.

Previous research has identified various 'direct ecosystem-drivers' (*sensu* Millenium Ecosystem Assessment) which affect ecosystem services and the ecosystem functions underpinning them at local scales. These include biodiversity (Cardinale *et al.* 2011; Balvanera *et al.* 2014), topography (Lavorel *et al.* 2011), soil conditions (Adhikari & Hartemink 2016) and land-use (DeFries *et al.* 2004; Chan *et al.* 2006; Lavorel *et al.* 2011). Many of these factors, termed ecosystem drivers hereafter, have contrasting effects on different services, promoting some while reducing others (Foley *et al.* 2005; Bennett *et al.* 2009; Anderson *et al.* 2009;

Raudsepp-Hearne *et al.* 2010; Lavorel *et al.* 2011), resulting in spatial segregation of the delivery of different services (Lavorel *et al.* 2011; Qiu & Turner 2013; 2015). Such trade-offs are often seen as problematic, as they limit the possibility for high ecosystem multifunctionality at the scales at which the trade-offs are observed (Chan *et al.* 2006; Bennett *et al.* 2009). However, various authors have successfully identified landscape configurations of a certain ecosystem driver (often land-use) that minimize these trade-offs, thus promoting landscape ecosystem multifunctionality (e.g. Polasky *et al.* 2008; Nelson *et al.* 2008). Here we build upon these findings by making the general prediction that *due to* trade-offs at smaller spatial scales, spatial variation in any ecosystem-driver ('heterogeneity') allows different services to reach high levels in different sites, thereby promoting multifunctionality at larger spatial scales. This phenomenon we term the '*multifunctional mosaic effect*'. While similar to earlier verbal arguments (Raudsepp-Hearne *et al.* 2010; Lavorel *et al.* 2017), this idea has not previously been theoretically formalized nor empirically demonstrated, limiting our understanding of how common positive heterogeneity-multifunctionality relationships are, and under which circumstances they most likely occur. General rules on ecosystem service supply as described by the multifunctional mosaic effect are currently lacking (Bennett *et al.* 2009), but could greatly aid the development of policies promoting ecosystem multifunctionality.

To illustrate the multifunctional mosaic effect, we consider two hypothetical cases. In the first, where the multifunctional mosaic effect is absent, all relevant ecosystem services respond identically to an ecosystem-driver (a low 'service-response-variance' or SRV, Fig. 1A), exemplified here with land-use intensification. As a result, land-use intensification diminishes all services, and heterogeneity does not determine landscape multifunctionality. An example of such a scenario includes drylands, where overgrazing reduces the provisioning of multiple services (Kairis *et al.* 2015). At the other extreme, where there is a strong multifunctional mosaic effect, ecosystem services show highly contrasting responses to the ecosystem-driver (high SRV, Fig. 1B), causing trade-offs. For example, agricultural land-use intensification typically promotes food production but diminishes cultural services (e.g. Lavorel *et al.* 2011; Allan *et al.* 2015). In such cases, landscapes containing locations with differing ecosystem-driver levels (high heterogeneity) complement each other in service provisioning, leading to greater multifunctionality (multifunctional mosaic effect) (Fig. 1B). For simplicity, our framework ignores interactions between landscape units such as the between-patch movement of ecosystem service providers (e.g. pollinators), which may modify the multifunctional mosaic effect. While rare, published examples of cases where landscape heterogeneity does (van der Plas *et al.* 2016) or does not always (Crouzat *et al.* 2015; Lavorel *et al.* 2017) promote landscape multifunctionality exist. We hypothesize that the multifunctional mosaic effect can resolve the paradox of such seemingly contrasting findings, thereby helping to synthesize our understanding of landscape-scale multifunctionality.

We investigated the multifunctional mosaic effect using simulation analyses of both theoretical data (to identify general conditions under which heterogeneity drives landscape-scale multifunctionality) and empirical data (to illustrate these rules in a case study). Using theoretical data, we constructed landscapes consisting of multiple sites varying in an ecosystem-driver, which could represent any factor driving ecosystem functioning (e.g. the presence of a keystone species, soil type). Various scenarios were analyzed, differing in the extent to which ecosystem-drivers caused trade-offs among ecosystem services, and we tested how this affected the relationship between heterogeneity and landscape multifunctionality. We then analyzed empirical data from German agricultural grasslands to investigate how relationships between heterogeneity in land-use intensity and landscape multifunctionality varied among scenarios, which differed in the ecosystem functions that were desired. We expected that positive effects of heterogeneity in land-use intensity would be strongest in scenarios including both ecosystem services responding positively (e.g. fodder production) and negatively to land-use intensification (e.g. flower cover).

MATERIALS AND METHODS

Theoretical simulations

With theoretical simulations, we created artificial landscapes consisting of plots varying in an ecosystem-driver, and hence in levels of multiple ecosystem services, to investigate to what extent positive relationships between heterogeneity and landscape multifunctionality arise when any type of ecosystem-drivers causes trade-offs among ecosystem services. We did this in five main steps, outlined in more detail in Fig. 1 and the following paragraphs. First, we created 1000 'scenarios' differing in the extent to which 5 ecosystem services varied in their correlation with an 'ecosystem-driver'. Next, within each scenario, 1000 simulated landscapes were created, each consisting of 5 plots differing in the ecosystem-driver and hence in ecosystem service values. For each landscape, 'ecosystem-driver heterogeneity' and landscape-multifunctionality were quantified, and we then quantified how ecosystem-driver heterogeneity affected landscape-multifunctionality ('heterogeneity-effect'). Finally, using linear models, we investigated how heterogeneity-effects were related to SRV values. We performed each of these steps in three sets of simulations, differing in the distribution of correlation strengths between the ecosystem services and the ecosystem-driver. In all simulations, the mean correlation-coefficient was 0, but the standard deviations varied and were 0.1, 0.2 and 0.5 in simulation 1, 2 and 3 respectively. Hence, in simulation 1, relationships between ecosystem services and the ecosystem-driver were generally weak, whereas in simulation 3, relationships were stronger and both positive and negative. These different simulations allowed to investigate how the general strength of service-driver relationships affected the multifunctional mosaic effect. All steps were carried out using R3.2.3 (R Core Team 2012).

In the first step of our simulations, we created 1000 'scenarios' varying in the extent to which an ecosystem-driver caused trade-offs among ecosystem services (see Fig. 1 for two extreme scenarios). To do this, we assumed a uniform distribution for the ecosystem-driver (range: 0-3, so $U(0,3)$. Other ranges would be mathematically equivalent) and simulated 5000 values, corresponding to 5000 "plots". This ecosystem-driver represents any factor driving ecosystem services, e.g. climate, the abundance of a keystone species, community composition, or land-use intensity. Furthermore, plots varied in their values of five hypothetical, standard-normally ($N(0, 1)$) distributed ecosystem services. In each scenario, these ecosystem service values were correlated with the ecosystem-driver according to a randomly assigned correlation-coefficient, with the correlation-coefficients coming from a distribution of either $N(0, 0.1)$, $N(0, 0.2)$ or $N(0, 0.5)$ (simulations sets 1-3, see above) and being constrained between -1 and +1. Next, using the ecosystem driver values and the correlation-coefficients between the ecosystem driver and the ecosystem services, we calculated ecosystem service values for each plot as: $ES_{i,j} = r_i \cdot ED_j + \varepsilon_i$, where $ES_{i,j}$ is the value of the *i*-th ecosystem service in plot *j*, r_i is the correlation-coefficient by which the *i*-th ecosystem service correlates with the ecosystem driver, ED_j is the ecosystem driver value in plot *j*, and ε_i is an error term, drawn from the distribution $N(0, (1 - [r_i]))$.

Because relationships between the ecosystem-driver and ecosystem services varied among scenarios, the key difference among scenarios is the extent to which the ecosystem-driver causes trade-offs among services. To quantify to what extent they did so, we calculated the SRV (see Introduction), using four steps. Firstly, we standardized ecosystem service values between zero and one: $SES_i = \frac{EF_i - \min(ES)}{\max(ES) - \min(ES)}$, with *SES* indicating the scaled ecosystem service, *ES* indicating unscaled ecosystem service and $\min/\max(ES)$ respectively indicating the minimum/maximum raw values of ES. This ensured that all services had the same range and a similar influence on landscape multifunctionality. Next, we converted all *SES* values to 'dummy ecosystem service' variables (*DES*) consisting of only 0 and 1 values, where a 1 indicates whether the original *SES* value was above threshold value *T* (which was 0.9 in main analyses, see 'Quantifying landscape multifunctionality' heading) and a 0 below it. Thirdly, we calculated the correlation-coefficient between each *DES* variable and the ecosystem-driver. Finally, we quantified the SRV by calculating the variance among these correlation-coefficients.

In the second step, we created 1000 landscapes within each scenario. Each consisted of a random combination (without replacement) of five (of the 5000 in total) plots. Due to the differences in ecosystem driver and service values among plots, the landscapes varied in average ecosystem-driver values, ecosystem driver-heterogeneity and hence in landscape multifunctionality.

In the third step, these variables were quantified within each scenario and for each landscape. Average ecosystem-driver values ('driver-average') were calculated as the mean of ecosystem-driver values across the five component plots of the landscape. Heterogeneity in the ecosystem-driver ('driver-heterogeneity') was quantified as the coefficient of variation in the ecosystem-driver across the plots. Landscape multifunctionality was quantified by adjusting a well-established approach of quantifying local-scale multifunctionality (Gamfeldt *et al.* 2007), where it is calculated as the number of ecosystem functions in a plot with values above a certain threshold. In our case, following van der Plas *et al.* (2016), we quantified landscape multifunctionality (*LMF*) as the number of services exceeding a threshold value in at least one of the (five) plots forming a landscape: $LMF = \sum_{i=1}^{n} \begin{cases} 1 \max(SES_{i,j}) \geq T \\ 0 \max(SES_{i,j}) < T \end{cases}$. Here, *n* is the number of services, 1 is the value by which an ecosystem service *i* contributes to multifunctionality when exceeding the threshold T (expressed as 0.9 multiplied with the 97.5th percentile; hence we consider a service value 'high' when it exceeds 90% of the outlier-removed maximum) and $\max(SES_{i,j})$ is the maximum value of ecosystem service *i* across the plots present in landscape *j*. This metric was chosen as it does not treat ecosystem services as substitutable: all are required to obtain maximum multifunctionality (Gamfeldt *et al.* 2007).

In the fourth step, we investigated the relationships between ecosystem-driver-heterogeneity and landscape-multifunctionality. We ran a multiple regression analysis for each scenario, with landscape-multifunctionality as the response and the driver-heterogeneity and driver-mean as predictors. We then quantified the standardized effect of ecosystem driver-heterogeneity, termed 'heterogeneity-effect' hereafter.

Finally, we investigated the relationship between this heterogeneity-effect and the SRV among scenarios, using simple linear regressions. A strong, positive relationships would indicate that in those scenarios where ecosystem-drivers caused strong trade-offs (high SRV), effects of heterogeneity on landscape-multifunctionality (heterogeneity-effects) were highest.

We performed additional analyses to investigate the sensitivity of our results to the multifunctionality threshold level, and the number of sites within a landscape. In these, we quantified landscape multifunctionality based on thresholds of 80% or 95% of the outlier-free maximum, and in landscapes consisting of 2 or 10 plots (As there were only 50 actual plots per region, more than 10 plots per landscape would result in many similar landscapes).

Empirical study

Study design

We used grassland plots from the three regions of the German Biodiversity Exploratories project (www.biodiversity-exploratories.de), which was established to study relationships between land-use intensity (LUI), biodiversity and ecosystem functioning. The South West region is the UNESCO Biosphere Area Schwäbische Alb, the Central region is in and around National Park Hainich, and the UNESCO Biosphere Reserve Schorfheide-Chorin is the North East region (see also Table S1). The Schwäbische Alb and Hainich NP are hilly regions with calcareous bedrock, while the Schorfheide is flatter, with a mixture if sandy and organic soils (Fischer *et al.* 2010 for details). Within each region, 50 grassland plots, measuring 50x50m, were established. Plots were selected to span the full range of LUI in Central European grasslands (Fischer *et al.* 2010), and thus vary greatly in their fertilizer inputs, mowing frequency and grazing intensity, while minimizing variation in potentially confounding factors such as soil type.

Land-use intensity

Data on the three LUI components, fertilization, mowing and grazing, was collected annually using a questionnaire sent to the managers of the plots (Blüthgen *et al.* 2012). Fertilization intensity was quantified as the amount of nitrogen addition, mowing frequency as the annual number of mowing events, and grazing intensity as the number of livestock units x the number of days of grazing. The different LUI components were standardized by dividing them by their regional means and LUI was quantified as the sum of these transformed components (Blüthgen *et al.* 2012).

Ecosystem function/service data

14 different ecosystem functions or properties ('ecosystem functions' hereafter), indicative of different ecosystem services, were measured in each plot. These include shoot biomass (indicative of fodder production), forage quality (fodder quality), potential nitrification

(nitrification rate), root decomposition (nutrient cycling rate), soil carbon stock (carbon storage), root biomass (belowground productivity), phosphorous retention index (nutrient cycling and water quality), mycorrhization (nutrient cycling), soil aggregation (soil quality), natural enemy abundance (pest control), lack of pathogen infection (plant health), pollinator abundance (pollination), flower cover (aesthetic appeal) and bird diversity (conservation value/appeal to birdwatchers). We used Multivariate Imputation by Chained Equations (MICE) to replace missing values (104 out of the 2100 values), using the 'mice' R package (Van Buuren & Groothuis-Oudshoorn, 2011). As soil properties potentially confound relationships between land-use and ecosystem functioning, we utilized data on five key soil covariables: soil depth, pH and soil sand, silt and clay content, as well as data on seven other environmental covariates: mean annual temperature, precipitation, average elevation, variability (standard deviation) in elevation, average slope, standard deviation in slope, and aspect. For details on these measurements, we refer to Hijmans *et al.* (2005) and Allan *et al.* (2015).

We then calculated 'environment-corrected' values for each ecosystem function. This was done using a linear mixed models, with each ecosystem function as the response, the twelve environmental covariables as predictors and region as a random factor. Environment-corrected ecosystem function variables were then quantified as the residuals from these models and used in further analyses. We also performed sensitivity analyses with raw ecosystem function values, where we either did not correct for environmental variation, or where we corrected for it when simultaneously investigating ecosystem function-LUI relationships (see below).

Statistical analysis

To investigate whether land-use heterogeneity effects on landscape multifunctionality are strongest in cases where LUI caused trade-offs among component functions of multifunctionality, we simulated 1000 scenarios. In each, landscape multifunctionality was based on a random subset of five out of a selection of 10 measured ecosystem functions, so that scenarios differed in their SRV. SRV was quantified by first correlating LUI with a) environment-corrected ecosystem functions (main analysis), or b) non-environment corrected ecosystem functions (sensitivity analysis 1), or c) by regressing uncorrected ecosystem function data to both LUI and the covariates described above (sensitivity analysis 2). SRV was then calculated as the variance of the correlation coefficients, or the variance of the standardized regression coefficients of LUI (in sensitivity analysis 2). As four of the 14 functions, natural enemy abundance, pollinator abundance, lack of pathogen infection and bird diversity, are likely partly driven by landscape context, for which data was lacking, we did not include these in the main analyses. However, we also performed a sensitivity analysis that included these functions. In each scenario, landscapes were simulated by randomly drawing, without replacement, five plots from within the same region. In each of the three regions, 1000 landscapes were simulated and in these we quantified several variables. Firstly, we quantified landscape multifunctionality using the same methodology as in our theoretical simulations, with the only difference that ecosystem functions were not standardized within the global dataset, but within regions. This ensured that within each region, each ecosystem function had similar variance and hence a similarly strong impact on ecosystem multifunctionality. LUI was quantified at the landscape-scale as the average LUI value of the local plots forming the landscape. Land-use heterogeneity (LUH) was quantified as the coefficient of variation in LUI across plots within a landscape. Hence, LUI and LUH were quantified in the same way as 'ecosystem-driver means' and 'ecosystem-driver heterogeneity' in the theoretical simulations. We then assessed the standardised effect of LUH on landscape multifunctionality ("heterogeneity-effect") using a multiple regression analysis, where landscape multifunctionality was the response variable, and LUH and LUI the predictors. In the sensitivity analysis 2, where the SRV was based on regressions and ecosystem functions were simultaneously predicted by LUI and the covariates (related to soil, altitude and climate), we also included average covariate values in the multiple regression on landscape multifunctionality. We investigated whether scenarios with the highest SRV displayed the strongest effects of heterogeneity on landscape multifunctionality, using linear regressions. We investigated the sensitivity of these results, by repeating the analyses based on multifunctionality variables quantified using threshold levels of 80 or 95% (instead of 90%) of the outlier-removed maximum and by repeating the analyses based on landscapes consisting of 2 or 10 plots.

Finally, we investigated relationships between LUH and landscape multifunctionality in a scenario that reflects a typical 'agricultural production and ecotourism' landscape objective. We did this by repeating the above analysis, with the only difference that multifunctionality was quantified in a single scenario only, where functions related to both agricultural production and ecotourism were valued, namely: shoot biomass, forage quality and flower cover.

RESULTS

Theoretical relationships

Our results showed that the effects of heterogeneity on landscape multifunctionality were strongest when (i) ecosystem services responded strongly to ecosystem-drivers (compare the SRV gradient of Fig. 2, panels A, B and C), and (ii) ecosystem services varied greatly in their response to the ecosystem-driver (high SRV) (see regression lines in Fig. 2A-C). Specifically, when ecosystem services generally responded weakly to the ecosystem-driver (Fig. 2A,B), and these weak responses varied little (SRV=0), heterogeneity had a slightly negative to slightly positive effect on landscape multifunctionality. When SRV increased, heterogeneity had a more positive effect on landscape multifunctionality, although these effects were still relatively weak, with standardized effects around 0.08 and 0.3 for the highest SRV values in simulation 1 (Fig. 2A) and 2 (Fig. 2B) respectively. When ecosystem services responded strongly to the ecosystem-driver (simulation 3, Fig. 2C), the heterogeneity effects became more strongly positive, with standardized effects almost maximal (around 0.9) for the highest SRV values. Hence, in such cases, landscape multifunctionality was almost completely determined by heterogeneity.

Sensitivity analyses showed that these results generally hold in landscapes composed of fewer or more sites, and when multifunctionality is quantified based on different thresholds (Table 1). The exception to this is simulation 1, where ecosystem services responded weakly to the ecosystem-driver. Here, multifunctional mosaic effects became even weaker in landscapes consisting of fewer or more sites than in the default scenario, or when the threshold level of high service provisioning was set lower. In summary, our results formalize the idea that heterogeneity can promote landscape-scale multifunctionality, but only when an ecosystem-driver has strong and contrasting effects on different individual ecosystem services.

Empirical data: random multifunctionality scenarios

Our analyses of empirical data showed that heterogeneity in land-use intensity promotes landscape multifunctionality in real-world grasslands. Relationships (*r*-coefficients) between individual ecosystem functions/services and LUI were on average close to 0, with a standard deviation around 0.2 (although the standard deviation was higher in the South West region) (Fig. 3A), the value that was modeled in theoretical simulation 2. Hence, we expected positive, albeit weak relationships between the SRV and heterogeneity-effects (but a slightly stronger relationship in the South West region), mirroring the relationship in theoretical simulation 2 (Fig. 2B). In agreement with this, we consistently found positive relationships between SRV and heterogeneity-effects in all three regions (Fig. 3B, Table 1). Hence, heterogeneity in LUI most strongly promoted landscape multifunctionality when ecosystem functions showed highly contrasting responses to land-use intensification. With only one exception (landscapes consisting of fewer plots in the North East region, where the multifunctional mosaic effect was non-significant), these results did not change qualitatively when landscapes contained fewer or more plots, or when multifunctionality was based on different thresholds (Table 1). There were, however, some quantitative differences. Most notably, effects of SRV on landscape multifunctionality were generally weaker when landscape multifunctionality was quantified using a lower threshold, but stronger when it was based on a higher threshold (Table 1). Our results hardly changed when functions that may be dependent on surrounding landscape characteristics were included, and were rather insensitive to whether/how correction for environmental covariates was performed (Table S2).

Empirical data: 'real-world' multifunctionality

In our investigation of how landscape multifunctionality is related to LUH in a scenario in which both ecosystem functions related to grassland forage production and ecotourism were considered desirable, we found contrasting responses of these functions to LUI, with SRVs of 0.089 (South West) and 0.069 (Central) and 0.044 (North East) (Fig. 4). Hence, we expected heterogeneity to have a positive effect on landscape multifunctionality in all regions, although this should be weaker in the North East. Our results were in line with this: in all regions, LUH significantly promoted landscape multifunctionality, but this effect was somewhat weaker in the North East (Fig. 4). In addition, there was a significantly positive effect of average LUI on landscape multifunctionality in both the North East and Central region, because most individual ecosystem functions responded positively to LUI (Fig. 4). Heterogeneity effects were insensitive to correction for environmental covariates (Fig. S2,3).

DISCUSSION

Using both theoretical and empirical data, we showed that heterogeneity in any factor driving variation in ecosystem services, be it land-use, the dominance of a keystone species, soil factors, climate or altitude, can promote landscape multifunctionality, as long as the ecosystem-driver has strong effects on ecosystem services and causes trade-offs among them. Interestingly, the heterogeneous landscapes needed to promote multifunctionality are broadly analogous to the "land-sparing" landscapes proposed to maximize both food production and biodiversity (Phalan *et al.* 2011), through spatial separation of land-use. However, in our study, we compare landscapes comprised of a single land-use type (grassland) but varying in intensity (broadly similar to land-sparing) with those of a uniform intensity (broadly similar to land-sharing). This differs from the comparison of segregated intensive farmland and more natural ecosystems (land-sparing *sensu* Phalan *et al.* 2011) versus a fragmented mixture of low-intensity farmland and semi-natural habitat (land-sparing) that is common in the literature (Green *et al.* 2005). Thus, our analyses show that the benefits of separating landscape units for different purposes are not limited to the simultaneous maximization of food production and biodiversity, but extend to other combinations of ecosystem services, and to other types of landscapes, consisting of one land-use only.

Although our study demonstrated cases in which heterogeneity can drive landscape-scale multifunctionality, factors not studied here might also be important. For example, we did not incorporate non-linear responses of services to ecosystem-drivers, differences in landscape configuration (Tscharntke *et al.* 2005), desired spatial patterns or scale of ecosystem service supply, or interactions between landscape units, such as the movement of ecosystem service providers (Mitchell *et al.* 2014). Furthermore, while we defined landscape multifunctionality as the number of ecosystem services provided at high levels within at least one site in a landscape, other definitions may better represent stakeholder demands. Future studies should ideally define ecosystem multifunctionality based on reported stakeholder requirements regarding the type and spatial configuration of service demand, and based on the supply-benefit relationship of ecosystem services (Manning *et al.* 2018). Hence, extending our work to incorporate ecosystem processes occurring at the landscape scale (e.g. hydrological flows and animal movements), as well as tailored metrics of landscape multifunctionality, would likely yield further insights.

Importantly, we also found that if the responses of ecosystem functions to an ecosystem-driver are weak or hardly vary, then heterogeneity does not promote landscape multifunctionality. This case occurred in North East German grasslands. Although we could not identify which factors were important for a high landscape multifunctionality, unmeasured landscape features, e.g. variation in soil types (peat-based versus sandy soil), may play a role. Other aspects of heterogeneity may additionally promote ecosystem multifunctionality through the same principles as described above, especially if they promote the diversity of ecosystem service providers (Benton *et al.* 2003). This raises the question of how widespread and predictable positive relationships between landscape multifunctionality and heterogeneity are. Our simulations using theoretical data showed strongly positive relationships between effects of heterogeneity on landscape multifunctionality and the service-response-variance when services responded strongly to the ecosystem-driver (Fig. 2C), but weaker relationships in other cases (Fig. 2A,B). Most ecosystem functions that we measured had relatively weak relationships with land-use intensity, hence the moderate multifunctional mosaic effects (Fig. 3). In cases where ecosystem services are more tightly related to an ecosystem-driver (e.g. Lavorel *et al.* 2011), we expect stronger multifunctional mosaic effects. Furthermore, while we studied a single land-use and habitat type, heterogeneity and ecosystem service trade-offs are likely to be stronger in landscapes consisting of multiple land-use and habitat types, which can strengthen multifunctional mosaic effects. Indeed, much stronger trade-offs between ecosystem services are often found in studies performed across habitat types (e.g. Chan *et al.* 2006*,* Anderson *et al.* 2009), and a range of drivers including climate (Anderson *et al.* 2009), species presence (Hector & Bagchi, 2009) and nitrogen enrichment (Bradford *et al.* 2014) can cause these trade-offs. On the other hand, in real-world landscapes, heterogeneity within habitat types (e.g. grasslands) is often lower than in our simulated landscapes, as similar intensities of land-use often tend to be spatially clustered (e.g. high land-use intensity in valley bottoms, low land-use intensity in uplands; Lavorel *et al.* 2017), which could weaken multifunctional mosaic effects. Hence, we expect that multifunctional mosaic effects are especially relevant when managing landscapes consisting of multiple habitat types, with high variation both within and across habitat types. It is therefore necessary to explore a wider range of cases to test and potentially validate the full range of our theoretically predicted landscape mosaic effects.

An important finding of this study is that landscape heterogeneity can promote landscape-scale ecosystem multifunctionality. However, it should be noted that it only does so under specific conditions. Specifically, when ecosystem drivers have strong, contrasting effects on the different ecosystem functions that are desired in a landscape. This context-dependency, and the fact that the drivers of ecosystem services are often unknown, limits our capacity to develop simple recommendations regarding how to maximize landscape multifunctionality that applicable in wide range of situations. Nevertheless, the landscape mosaic principle presented here can inform landscape management, under certain conditions. For example, if it is known which ecosystem functions or services are desired from a landscape, and that some of these services (e.g. agricultural production) benefit from high levels of the ecosystem driver, and other services (e.g. biodiversity of charismatic species) do not, then it follows that promoting heterogeneity in an ecosystem driver (e.g. land-use intensity) might be beneficial. However, promoting heterogeneity could be counterproductive in cases where most desired services respond in the same direction to drivers, thus highlighting the need for a data-informed approach to landscape management.

In the longer term, the hypothesis of the landscape mosaic effect provides the foundation for work that could generate more exact predictions of multifunctional mosaic effects in particular cases, although generating these predictions is not straightforward and only possible with detailed information on ecosystem services and their drivers. As a roadmap to apply the multifunctional mosaic effect framework for the management of landscapes to promote multifunctionality, we propose four main steps for future projects, though we note that each of these is challenging and substantial. First, stakeholders should be involved to decide which ecosystem services are required, and which levels of supply are desired. Secondly, relationships between factors that could (*i*) be feasibly manipulated by landscape managers (e.g. the proportion of habitat types such as grassland, cropland and forest, or forest tree species composition) and that (*ii*) influence multiple ecosystem services, should be described. In many cases, this information is already available. For example, continental-scale efforts linking ecosystem service provisioning to different habitats (Maes *et al.* 2016) can be used to assess whether landscapes consisting of multiple habitat types are more multifunctional than homogeneous landscapes. In other cases, new field campaigns are required to generate the basic knowledge needed to investigate heterogeneity-multifunctionality relationships. Thirdly, once the required data are available, simulations as carried out in this study (which are added in the Supplementary Material), can be used to investigate if, and how strongly, heterogeneity will landscape multifunctionality. Finally, these insights can support decisions regarding the conservation or restoration of landscape compositions promoting multifunctionality, e.g. by informing policy, such as the European Union greening measures, which specify the proportion of land to be devoted to different land uses (Pe'er *et al.*, 2016). As noted before, various factors, such as interactions between landscape units or the dispersal of ecosystem service providers, are not taken into consideration in our analyses. Hence, while following the above roadmap roadmap is useful for guiding recommendations on landscape compositions, ecosystem service assessments in realized landscapes are required to see if actual service provisioning deviates from predictions, and, if so, which mechanisms have caused deviations. By doing so, increasingly accurate predictions of landscape service provisioning can be developed, and potentially used in the challenging task of promoting the conservation, restoration and/or creation of multifunctional landscapes.

AUTHORS' CONTRIBUTIONS

FvdP, PM, MF and EA designed the concepts and analysis of this study and FvdP analyzed the data. FvdP and PM wrote the paper, all other authors provided data and commented on the paper. All authors gave final approval for publication.

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DATA ACCESSIBILITY

Data available via Figshare DOI: http://doi.org/10.6084/m9.figshare.6870788 (van der Plas et al 2018)

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Fig. 1. Hypothetical relationships between landscape heterogeneity and multifunctionality. **A**: Two ecosystem services respond similarly to land-use intensity (LUI). As a result of this low ‘service-response-variance’, the services correlate positively. Homogeneous landscapes consisting solely of high (yellow) or low LUI (blue) sites support either both or no services at high levels, while a heterogeneous landscape supports both, in some places. **B**: Two ecosystem services respond differently to LUI. As a result of this high ‘service-response-variance’, the services trade-off against each other. Homogeneous landscapes consisting of

sites with uniformly high or low LUI support only one service, while heterogeneous landscapes support both services at high levels, but in different places.

Fig. 2. The positive effects of heterogeneity on landscape multifunctionality increase with a high variability in the responses of ecosystem services to an ecosystem-driver (service-response-variance or SRV). **A-C**: The relationship between heterogeneity effects and SRV becomes stronger when the ecosystem-driver has strong effects on ecosystem services: standard deviation of *r* values between ecosystem services and the ecosystem-driver varies among simulations, from 0.1 (simulation in **A**), 0.2 (**B**) and 0.5 (**C**). Relationships between the ecosystem-drivers and ecosystem services of two scenarios of simulation **B** (highlighted in orange) are shown in panel **D** (low SRV) and **E** (high SRV).

Fig. 3. Positive effects of heterogeneity on landscape multifunctionality increase with a high variability in the responses of ecosystem services to land-use intensity (LUI). **A**: Distribution of *r*-coefficients of multiple ecosystem functions with LUI. Overall mean and standard deviation are shown in the figure. Means and standard deviations within regions are respectively: 0.131 and 0.364 (South West, blue bars), 0.042, 0.126 (Central, red) and 0.037 and 0.183 (North East, green). **B**: In empirical landscapes, land-use heterogeneity most positively affects landscape multifunctionality in scenarios where ecosystem services vary strongly in their response to land-use intensity (high service-response-variance).

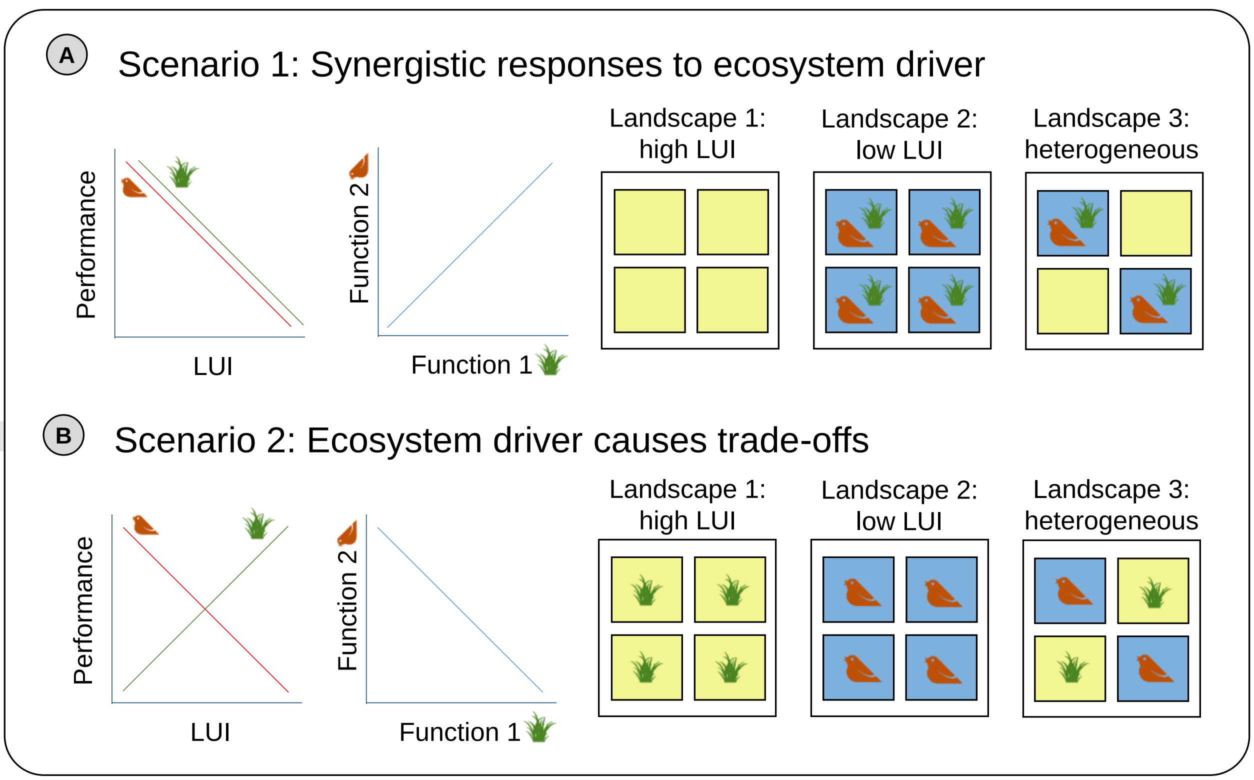
Fig. 4. Effects of landscape-level land-use intensity (LUI) and heterogeneity (LUH) on grassland multifunctionality (MF) in three German regions. Yellow bars: standardized LUI effects on individual ecosystem functions (EF) (service-response-variance = SRV). Red bars: standardized LUI effect on MF. Blue-green bars: standardized LUH effects on MF.

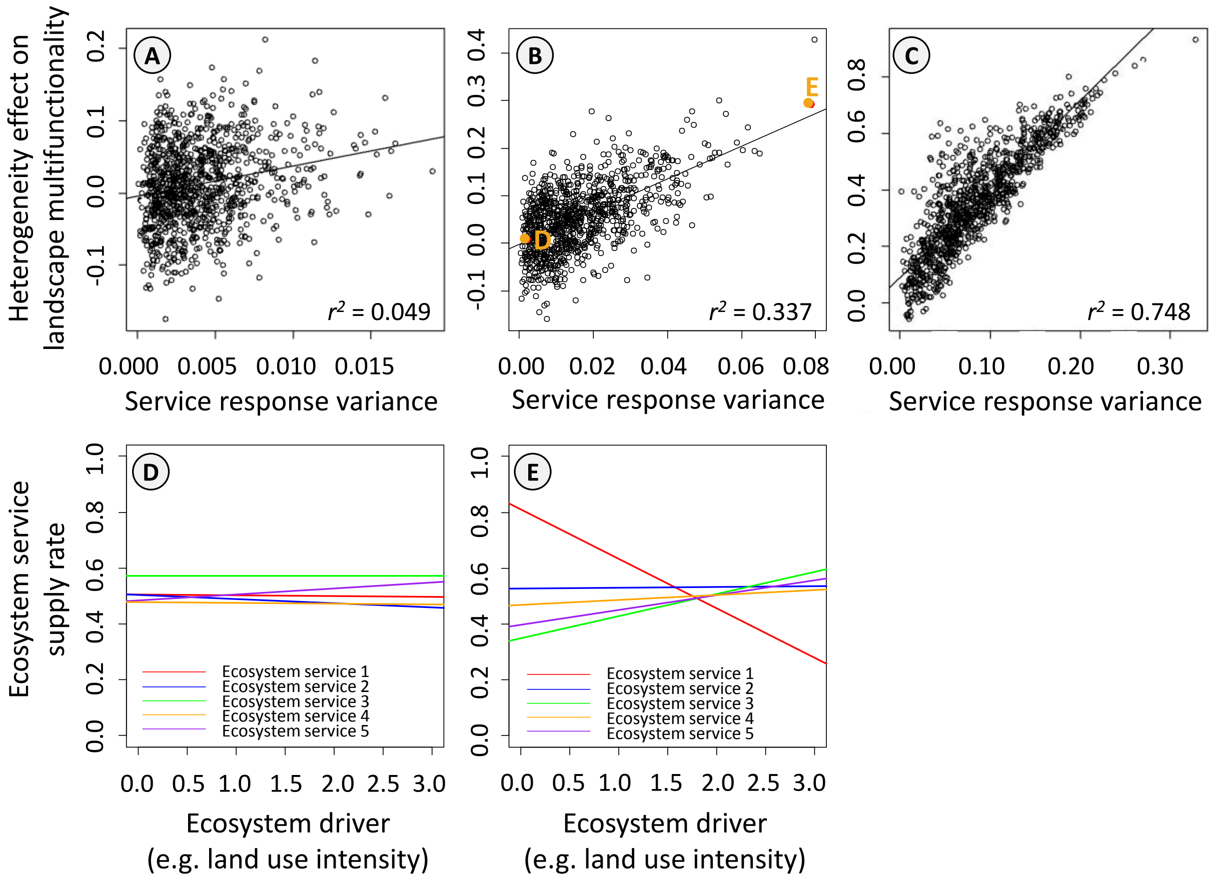
Table 1. Relationships between the service-response-variance (SRV) and heterogeneity-effects, in main (bold) and sensitivity analyses. Sd: standard deviation of *r*-coefficients between ecosystem services and the ecosystem-driver. Txx%: multifunctionality threshold level. Standardized effect: the standardized effect size of SRV on the heterogeneity-effect.

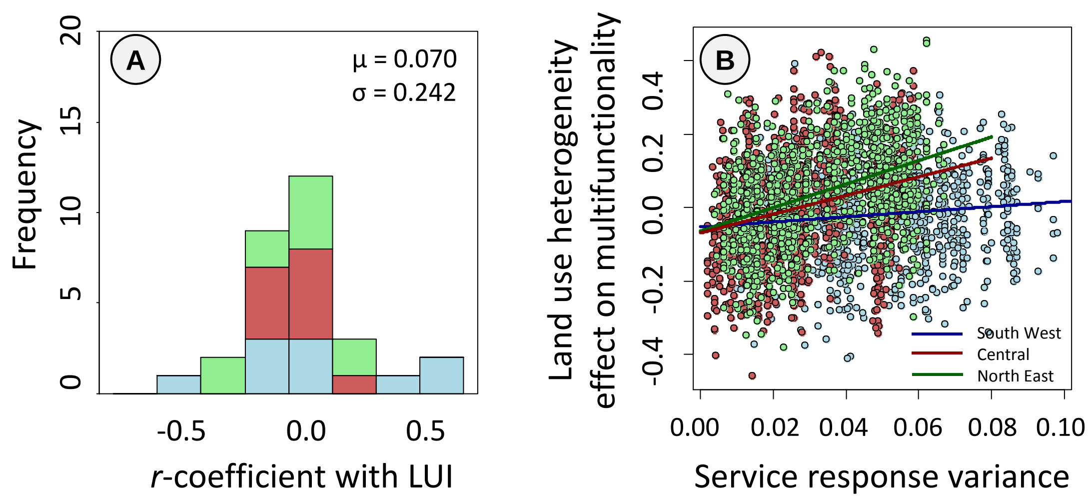
	Standardized effect	r^2	**Significance**
Theoretical Data			
Sd=0.1			
5 plots, T80%	0.131	0.016	<0.0001
2 plots, T90%	0.109	0.011	0.0005
5 plots, T90%	**0.220**	**0.048**	**<0.0001**
10 plots, T90%	0.144	0.020	<0.0001
5 plots, T95%	0.220	0.048	<0.0001
Sd=0.2			

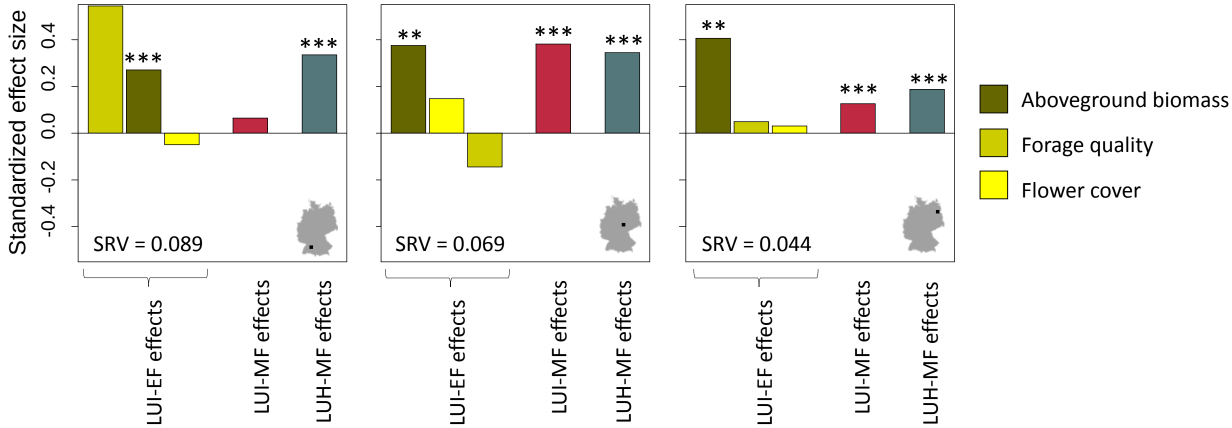
5 plots, T80%	0.548	0.299	<0.0001
2 plots, T90%	0.515	0.264	<0.0001
5 plots, T90%	**0.581**	**0.337**	**<0.0001**
10 plots, T90%	0.550	0.303	<0.0001
5 plots, T95%	0.524	0.274	<0.0001
Sd=0.5			
5 plots, T80%	0.863	0.745	0.0001
2 plots, T90%	0.835	0.698	0.0001
5 plots, T90%	**0.865**	**0.748**	**<0.0001**
10 plots, T90%	0.855	0.731	<0.0001
5 plots, T95%	0.848	0.718	<0.0001
Empirical data			
South West			
5 plots, T80%	0.330	0.108	<0.0001
2 plots, T90%	0.208	0.042	<0.0001
5 plots, T90%	**0.258**	**0.066**	**<0.0001**
10 plots, T90%	0.213	0.044	<0.0001
5 plots, T95%	0.443	0.195	<0.0001
Central			
5 plots, T80%	0.317	0.100	<0.0001
2 plots, T90%	0.348	0.120	<0.0001
5 plots, T90%	**0.477**	**0.227**	**<0.0001**

10 plots, T90%	0.447	0.199	<0.0001
5 plots, T95%	0.603	0.363	<0.0001
North East			
5 plots, T80%	0.189	0.035	<0.0001
2 plots, T90%	-0.001	-0.001	0.9690
5 plots, T90%	**0.140**	**0.019**	**<0.0001**
10 plots, T90%	0.296	0.087	<0.0001
5 plots, T95%	0.209	0.043	<0.0001




A
B
C
D
E
Heterogeneity effect on landscape multifunctionality
Service response variance
r2 = 0.049
r2 = 0.337
r2 = 0.748
Ecosystem service supply rate
Ecosystem driver (e.g. land use intensity)
Ecosystem service 1
Ecosystem service 2
Ecosystem service 3
Ecosystem service 4
Ecosystem service 5


A
μ = 0.070
σ = 0.242
Frequency
r-coefficient with LUI
B
Land use heterogeneity effect on multifunctionality
Service response variance
South West
Central
North East


Standardized effect size
-0.4 -0.2 0.0 0.2 0.4
***
***
SRV = 0.089
**
***
***
SRV = 0.069
**
***
***
SRV = 0.044
LUI-EF effects
LUI-MF effects
LUH-MF effects
Aboveground biomass
Forage quality
Flower cover