The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation

Lindemann-Matthies, P; Junge, X; Matthies, D
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Abstract

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The conservation of biodiversity critically depends on the value that humans attach to it. Apart from an ecological and economic value, an aesthetic value has often been assigned to biodiversity. However, it is not known whether lay people appreciate the diversity of species and not just certain individual species or nature as a whole. We studied in a series of experiments and field studies people's perception and appreciation of species diversity. We presented meadow-like arrays of different species richness and evenness but random species composition to lay people and asked them to estimate plant species richness and rank the arrays by attractiveness. The experiments were complemented by two larger-scale field studies using natural meadows. Both in the experiments and the field studies the mean perception of species richness by people increased with true species richness, but was slightly overestimated at low and increasingly underestimated at high diversity levels. Lay people's aesthetic appreciation of both the experimental grassland arrays and the natural meadows increased with true species richness. Communities consisting of the same number of species were perceived to be more species-rich and were appreciated more when their evenness was high. Our results demonstrate that plant diversity in itself is attractive to humans. The current reduction of the diversity of grasslands due to intensification of management may thus reduce the attractiveness of regions where grasslands are a dominant feature of the landscape. This could have negative consequences for tourism and may add an economic argument for the conservation of biodiversity in grasslands.
Introduction

Human alterations of the environment have resulted in the loss of biodiversity both at the global and at the regional scale (MEA, 2003; Thomas et al., 2004; Balmford and Bond, 2005). Much of the remaining biodiversity will survive only if humans choose to protect it and are willing to allocate funds for its conservation (Stokes, 2007). Thus, the conservation of biodiversity critically depends on the values that humans attach to it, which include ecological, economic, cultural, aesthetic, ethical and spiritual values (Edwards and Abivardi, 1998; Chapin et al., 2000; Saunders, 2003; Trombulak et al., 2004; Saunders et al., 2006). All of these values have validity, motivating different groups of people to support conservation, therefore none should be discarded (Hector et al., 2001; Jepson and Canney, 2003). However, conservationists have devoted little attention to human biodiversity preferences, and it is poorly understood which components of biodiversity will appeal to people (Little et al., 2001; Stokes, 2007). A greater awareness of public preferences would allow a better prediction of the acceptance of biodiversity management measures, and facilitate the development of suitable ways of communicating these, hence increasing the likelihood of biodiversity management success (Fischer and van der Wal, 2007; Fischer and Young, 2007).

Recent studies have demonstrated the ecological importance of biodiversity. Experiments in which biodiversity was manipulated have shown that diversity influences many ecosystem functions (Hector et al., 1999; Tilman et al., 2001; Hooper et al., 2005; Spehn et al., 2005; Balvanera et al., 2006). Because of this link there is concern that the global reduction of biodiversity may diminish the capacity of ecosystems to provide society with a stable and sustainable supply of essential goods and services (Hooper et al., 2005; Spehn et al., 2005; Balvanera et al., 2006). Ecologists and economists have carried out valuation exercises to estimate the economic benefits of conserving biodiversity both at the global (Costanza et al.,
Apart from ecological and economic value, biodiversity has often been assigned an aesthetic value (Hector et al., 2001; Balmford et al., 2002a; Gobster et al., 2007) and the provision of aesthetic beauty has been included in the list of services provided by ecosystems (Daily, 1997; MEA, 2003; Chee, 2004; Wallace, 2007). It has also been suggested that the aesthetic benefits of biodiversity to humans should be considered in land management (Sanderson et al., 2004) and conservation (Swart et al., 2001; Jepson and Canney, 2003). However, while the importance of biodiversity for ecosystem functioning is well established, the importance of biodiversity for the aesthetic value of ecosystems is not known. The aesthetic value of certain species is one of the reasons often given for conservation (Kiester, 1997; Hector et al., 2001; Stokes 2007), but no studies to date have explicitly tested whether humans aesthetically appreciate species richness *per se* and not just certain species or nature as a whole. People's aesthetic appreciation could be influenced by both the actual and the perceived species richness of communities.

Little is known about how well people are able to perceive differences in species richness between communities (Little et al., 2001; Fuller et al., 2007), but people's ability to identify species - at least in wealthier countries - has been found to be very limited, which might also impede the perception of species richness (Balmford et al., 2002b; Bebbington, 2005; Pilgrim et al., 2008). The demonstration of a link between the diversity of a community and its aesthetic value could provide a further argument for the conservation of diverse communities. Natural scenes that are perceived as aesthetically pleasing are more likely to be appreciated and protected than those that are perceived as undistinguished or ugly, regardless of the less directly perceived ecological importance (Gobster et al., 2007).
Although there is a large body of research on visual aesthetic responses of humans to large-scale outdoor environments (overview in e.g. Ulrich, 1986; Kaplan and Kaplan, 1989; Ulrich, 1993; Kaplan et al., 1998), little is known about people’s responses to smaller units of vegetation, such as herbaceous plants (Ulrich, 1986; but see Akbar et al., 2003). Road users in northern England liked best grass swards with flowering native herbs or occasionally mown grass swards with colourful flowering herbs for re-vegetation along roadside verges (Akbar et al., 2003). Similarly, colour slides that depicted aspects of wildflower meadows rich in biological diversity received high preference ratings by the participants of a study by Strumse (1996) on visual preferences for agrarian landscapes in western Norway. Recently, in-situ surveys in Switzerland have shown that species- and flower-rich field margins improved the aesthetic value of landscapes (Junge et al., 2009). The overall objectives of this study were to investigate whether people appreciate diversity and how well they can estimate it. We carried out two biodiversity experiments, in which meadow-like arrays consisting of different numbers of plant species grown in pots were presented to visitors of botanical gardens. People were asked to estimate the number of species and to rank the arrays by their attractiveness. In the experiments we used different random combinations of species for each species richness level and could thus separate the effects of species richness on perception and appreciation from those of species composition and identity (Huston, 1997; Tilman, 1997). As diversity has two main components, the number of species and species evenness, i.e. how well distributed abundance is among species within a community (Wilsey and Potvin, 2000), we also studied the effects of species evenness in a similar way. In addition, we studied the effect of different spatial distributions of species, another component of diversity (Díaz et al., 2006). Botanical gardens were used as settings for the experiments, as they provided water, space and shelter for the plants. The experiments allowed complete control over species richness, composition and evenness, but they were rather small. To study diversity effects in larger,
natural communities, we carried out two complementary field studies, in which the influence of the species richness of meadow communities on people's perception and aesthetic appreciation was investigated on a larger scale in natural settings.

We set out to investigate the following questions: (1) Can lay people accurately perceive the species richness of grassland communities? (2) Does aesthetic valuation of grassland communities increase with increasing species richness? (3) Are lay people's perceptions and aesthetic valuation influenced by the dominance structure (evenness) of a community and the spatial distribution of species?

**Materials and methods**

*Design and data collection*

For the experiments several thousand plants belonging to 69 typical species from grasslands and arable fields (54 forbs, 15 grasses) in central and western Europe were cultivated individually in square pots (9 x 9 cm). Grassland vegetation has a number of features that made it a suitable model for our studies. The biodiversity of meadow communities varies strongly, meadow plants are of relatively low stature, can be easily grown in high numbers and have therefore been frequently used in experiments on biodiversity–ecosystem functioning relationships (Naeem et al., 1994). In the experiments, a number of pots with plants were arranged in square arrays that gave the impression of a meadow and presented to the public in wooden frames on tables. The species presented in each array were selected at random. In all experiments, study participants were asked to assess the number of plant species present in each array and to rank the arrays by attractiveness. A ranking procedure was chosen to force participants to make clear statements about the attractiveness of the
arrays. Each day a new selection of species was presented to make it possible to separate the effects of species diversity from those of species identity.

In experiment 1, five arrays of different species richness (1, 2, 4, 8, and 16 species), each consisting of 49 pots, were presented simultaneously in random order. Within an array the number of individuals of each species was as similar as possible to result in 49 pots overall and the spatial distribution of the species was random. We presented the arrays in summer 2002 on 20 days to 275 randomly selected visitors of the Botanical Garden and of the University Hospital in Marburg, Germany. The botanical garden site was chosen for ease of logistics. Part of the experiment was carried out at the entrance to the hospital because we assumed that hospital visitors might be more representative of the general population than visitors to a botanical garden. However, there were no significant differences between visitors to the botanical garden and to the university hospital in their perception and appreciation of the arrays and we therefore pooled the data from both sites.

In experiment 2 and 3 we used similar array experiments in the Botanical Garden in Marburg to test the effects of varying the evenness (i.e. the degree to which species are equal in abundance) and the spatial distribution of species, keeping species richness constant. In experiment 2, we presented four arrays of constant species richness but different evenness (Shannon-Wiener evenness = 0.99, 0.88, 0.64 and 0.52), each consisting of 49 pots. Each array contained 16 species that were changed daily. We presented the arrays on 12 days in summer 2002 to 166 visitors of the Botanical Garden Marburg.

In experiment 3, the effects of the spatial distribution of plants were studied. Three arrays each consisting of 49 pots were presented together. Each array contained four species with nearly the same number of individuals (12, 12, 12, and 13), but in different spatial configurations: Aggregated (plants of each species in a compact, nearly rectangular patch),
random, or diagonal (individuals of each species in diagonal rows). We presented the arrays on 14 days to 204 visitors. Each day a new selection of species was presented.

Experiment 4 was set up to study the effects of higher species richness. It was similar to experiment 1, but each array consisted of 64 pots. In summer 2003 arrays with 4, 8, 16, 32, and 64 species were presented simultaneously on 20 days to 288 visitors of the Botanical Garden of the University of Zurich, Switzerland.

To study diversity effects in larger, natural communities, we carried out two complementary field studies, in which we asked people who passed field plots of different diversity near Zurich (500 m elevation) and Davos in the Swiss Alps, about their perception and valuation of these grassland ecosystems. In summer 2003 we delimited 72 meadow plots (2 x 2 m) of different plant species richness along waysides near Zurich using colored tape and presented them to 217 passers-by. Study participants were asked to look closely at three of the plots from predefined spots, to assess the number of plant species in each plot, and to rate the attractiveness of each plot using the scale of Swiss school marks (1 = least to 6 = most attractive). For each plot we recorded the identity of all vascular plant species and estimated their cover. To investigate effects of diversity in a different habitat, an analogous study was carried out in summer 2005 in meadows (1200 - 2300 m a.s.l.) in the Alps near Davos, Switzerland, using 24 plots of 1 x 25 m. We used a larger plot size in this study to investigate the effects of a higher number of species (since species number increases with area). Overall, 282 passers-by were asked to rate one of the plots.

In all data collection exercises, study participants were asked first to estimate plant species richness and then to rate attractiveness. To avoid bias, the purpose of the research was not revealed to the study participants. To ensure that the framing and wording of questions was always the same, a standardized written questionnaire was used in both the experiments and
the field studies. Study participants were asked to fill in the number of plant species they had estimated in each array or plot, and to fill in either the rank or beauty mark given to each meadow. The age and gender of the participants were also recorded. Furthermore, study participants were asked to self-estimate their taxonomic knowledge in comparison to that of the general public by ticking one of the possible answers of a five-step rating scale (very poor = 1, rather poor = 2, neither poor nor good = 3, rather good = 4, very good = 5).

The content validity of the items in the questionnaire was evaluated by a panel of five experts in environmental sciences. Based on their comments, the final items were formulated and tested in 2002 in a trial run during a full day in the botanical garden of Marburg. Moreover, a full day trial run was also conducted at each location of the two field studies. All pilot studies showed that the method was suitable to investigate people's perception and appreciation of plant diversity. On average, it took the participants 15 minutes to accomplish the task.

**Study participants**

In the experimental studies, the participants (60% women) were between 18 and 85 years old (Marburg: mean age = 43 years; Zurich: mean age = 42 years). Study participants considered their taxonomic knowledge of plants to be average compared to that of the general public (both Marburg and Zurich: mean = 3.2 on the five-step rating scale). In the two field studies, the participants (56% women) were between 18 and 89 years old (Zurich: mean age = 39 years; Davos: mean age = 52 years). Participants in these studies also considered their taxonomic knowledge of plants to be average (both Zurich and Davos: mean = 2.9 on the five-step rating scale).
Data analysis

For each individual array in the experiments and each plot in the field studies the mean estimated number of species and the mean rank (or mean mark in the field studies) were calculated. Because of the skewed distribution, geometric means were calculated for perceived species richness. The effects of true species richness, evenness, or spatial distribution in the experiments on perception and appreciation were analyzed by linear models in which the error term was the residual variation among the arrays, because each array represented a unique species composition. The residual variation among the arrays was due to the species composition of the arrays, i.e. the identity of the species in an array and the interactions between them, and its effect was tested against the residual variation among people's ratings.

The influence of perceived species richness on aesthetic appreciation in the experiments was analyzed by hierarchical linear models in which the effect of perceived species richness was fitted first and that of true species richness (as a factor) was fitted second to calculate the additional effect of true species richness. The contribution of both variables was evaluated as the proportion of the total sum of squares explained. In the field studies the contribution of perceived and true species richness was calculated in an analogous way.

To test whether the presence of an individual species had an effect on the aesthetic appreciation of an array that was not explained by its contribution to species richness, a variable coding for the presence/absence of this species was fitted after the effect of true species richness in a hierarchical linear model. The effect of the presence of each species was tested separately. Because of the limited number of different arrays, effects of interactions between particular combinations of species could not be tested explicitly.

Results

In the two diversity array-experiments in Marburg and Zurich the mean perception of species richness by visitors increased with true species richness, but was slightly overestimated at low and increasingly underestimated at high levels (Fig. 1a, b; Marburg: $F_{4,95} = 237.5$, $P < 0.001$; Zurich: $F_{4,95} = 29.4$, $p < 0.001$). A similar result was found for the field plots in Zurich (Fig. 1c, $r = 0.73$, $F_{1,70} = 80.9$, $p < 0.001$) and Davos (Fig. 1d, $r = 0.48$, $F_{1,22} = 6.4$, $p = 0.019$). The much lower correlation found in Davos was probably due to the restricted range of values of species richness, as there were no very species-poor plots. At the level of individual visitors, the number of species perceived also increased with species richness in both the experiments at Marburg ($r = 0.65$, $n = 1299$, $P < 0.001$) and Zurich ($r = 0.42$, $n = 1425$, $P < 0.001$).

In the evenness experiment, the perceived species richness increased with evenness, although the true species richness was always 16 species (Fig. 1e; $F_{3,44} = 11.1$, $p < 0.001$). In the spatial distribution experiment, in which four species were presented in equal abundance but in three aggregation patterns, visitors perceived higher species richness in diagonal and random patterns than in the aggregated pattern (Fig. 1f, $F_{2,39} = 6.5$, $p < 0.01$).

In parallel to the increasing number of perceived species in the array-experiments, the visitors’ mean aesthetic appreciation of the experimental grassland ecosystems also increased with true species richness (Fig. 2a, b; Marburg: $F_{4,95} = 71.1$, $p < 0.001$; Zurich: $F_{4,95} = 36.1$, $p < 0.001$). Similarly, in the field studies people’s appreciation of grassland plots increased with true species richness both in Zurich (Fig. 2c, $r = 0.75$, $F_{1,70} = 91.3$, $p < 0.001$) and in Davos with a more species-rich alpine vegetation (Fig. 2d, $r = 0.45$, $F_{1,22} = 5.6$, $p = 0.027$). The much lower correlation found in Davos may have been due to the fact that all plots were rated relatively high, because there were no plots that were very species-poor. In the experiments, the
appreciation of the best monoculture was always lower than the mean appreciation of the most species-rich arrays (Fig. 2a, b).

The number of species perceived explained a considerable part of the variation in appreciation of the experimental arrays and of the field plots (36 % - 76%, Table 1), except in the Davos field study (only 2%), where the relationship between perceived and real species richness was weakest (see Fig. 1 d). However, in most of the studies, the true number of species present explained a significant additional proportion of the variation (Table 1).

People’s appreciation of biodiversity was also influenced by the identity of species and their interaction within given diversity levels (significant effect of species composition, i.e. the individual arrays, on appreciation; Marburg: $F_{95, 1120} = 4.30, p < 0.001$; Zurich: $F_{95, 1255} = 5.50, p < 0.001$). Decomposing the composition term into contrasts for the occurrence of particular species showed that two species with colourful flowers (Papaver rhoeas and Linaria vulgaris) significantly increased people’s appreciation of plant communities, whereas several other species, in particular grasses, decreased it (Table 2).

Judged attractiveness also increased with evenness (Fig. 2e; $F_{3,44} = 8.1, p < 0.001$). This indicates that people appreciated arrays more if the species within them occurred in similar abundance than if arrays were dominated by a single or a few species. Because true species richness was in reality constant, the increase in judged attractiveness ($r = 0.46, F_{1,46} = 12.6, p < 0.001$) is likely due to the perception of enhanced species richness brought on by the effect of increased evenness (Fig. 1e). In the spatial distribution experiment the appreciation of the arrays marginally increased from clumped to random to diagonal patterns (Fig. 2f; $F_{2,39} = 2.88, p = 0.068$).

Discussion

Perception of species richness

Generally, people could differentiate between species-rich and species-poor plant communities. However, in both the experimental and field studies, people consistently overestimated plant species richness when it was low and underestimated it, when it was high. In contrast, in a study of urban greenspaces (Fuller et al., 2007) it was concluded that people can more or less accurately perceive species richness. However, results from that study are not strictly comparable, because people had to estimate species richness in broad classes. Our results suggest that people may not be able to realize the full species richness of diverse grassland communities, in particular, if evenness is low. At low evenness, species occurring at low frequencies might be easily overlooked and this could lead people to substantially underestimate species richness.

This misperception (too few species) by people of the species richness of communities in front of them is in strong contrast to the fact that when people are asked to estimate the number of species worldwide (Dunning, 1997) or in specific communities like alpine meadows or forests (Lindemann-Matthies and Bose, 2008), they usually overestimate it widely. Like misconceptions (Dunning, 1997; Lindemann-Matthies and Bose, 2008), such misperceptions of the number of species could potentially bias people's valuation of communities and thus their response to reports of species losses and their attitude to conservation.

Interestingly, in the experiments people’s ability to discriminate between levels of species richness dropped off as the true number of species increased, i.e. the differences in perceived species richness became smaller as the true number of species increased. This was particularly pronounced at the highest species levels (Fig. 1b). This finding could reflect a psychological
phenomenon in mental scaling. It has been shown that numerical processing obeys Weber's law, i.e. the discriminability of two numbers decreases as the magnitude of the numbers increase (Moyer and Landauer, 1967; Longo and Lourenco, 2007). This might have led to the observed underestimation of species richness when it is high.

Although in the experiment on the effect of spatial distribution the actual number of species was constant, the perceived species richness increased in the order: aggregated, random, diagonal pattern. When the pattern was diagonal, people may not have recognized the diagonal rows of individual of the same species, but may instead have been influenced by the distance between individuals of the same species in the vertical and horizontal directions, which was highest in this type of distribution, making this pattern most regular. Our results are in line with those of psychologists who found that regularly arranged items appear more numerous than the same number arranged randomly, and that random patterns are judged more numerous than clustered ones (Ginsburg and Goldstein, 1987).

**Appreciation of species richness**

Perceived species richness had a strong influence on people's aesthetic appreciation of communities. This was particularly clear in the evenness experiment, in which species number was held constant, but both the perceived species richness and the aesthetic appreciation increased with the evenness of the experimental communities. Similarly, the appreciation of the different types of spatial patterns increased with their perceived species richness, corroborating the result that perception and appreciation are related with each other even in the absence of co-varying true species richness. Interestingly, in several of the studies, the true number of species present explained a significant additional proportion of the
variation in appreciation, suggesting that people's appreciation may have been unconsciously influenced by true species richness.

The results from our two diversity manipulation experiments, the two diversity field studies and the evenness and spatial distribution manipulation experiments consistently showed that people found those communities most beautiful that were either most diverse or were perceived to be most diverse. These results are in line with those from a previous study in which people were asked to assemble their own favorite meadow patch by selecting 25 out of 780 local wild plants (54 species) that were displayed in flower pots. The patches created were very species-rich (mean = 17.2 species) and people explicitly stated diversity as their main assemblage criterion (Lindemann-Matthies and Bose, 2007). Recently, a study of greenspaces found a positive relationship between the psychological benefits of greenspaces and their biodiversity (Fuller et al., 2007). Because the design of our experiments was analogous to that of biodiversity–ecosystem functioning experiments (Tilman et al., 2001; Schmid et al., 2002) it allowed a separation of the effects of species diversity and identity. The higher aesthetic appreciation of species-rich communities was mainly due to diversity itself and not due to the presence of particular species.

Two mechanisms have been proposed to explain how biodiversity influences ecosystem functioning (Huston, 1997; Tilman, 1997; Loreau, 2000), and in particular productivity in experimental grasslands (Naeem et al., 1996) and natural ecosystems (Montès et al., 2008): (1) Different species use slightly different resources, and in species-rich communities more resources are used and productivity is thus higher ('niche complementarity'). Positive interactions among species may also contribute to this effect. (2) With increasing species richness the probability increases that species with a dominant negative or positive effect are included ('sampling effect', Huston, 1997). Both these phenomena potentially explain the
The greater aesthetic appreciation of species-rich vegetation by people. Different plant species have different morphological features that independently or in interaction may contribute to the overall appreciation of a community by people (a complementarity mechanism), and species-rich communities are more likely to contain species that are perceived as particularly beautiful and that therefore might dominate the overall appreciation. Inspection of Fig. 2 indicates that the upper bound of appreciation increased with species richness, i.e. species-rich systems were more appreciated than even the most appreciated species in monoculture. However, not all species could be presented in monocultures, and it can therefore not be excluded that a particular attractive species in monoculture might have been rated higher than the high diversity mixtures. Still, our results indicate that the so-called sampling effect could not fully explain the species richness effect on appreciation, and that complementary effects of several species were more important for the aesthetic appreciation of a community than dominance effects of a single species (cf. Tilman et al., 2001). This is an important result, because it provides an aesthetic argument for the conservation of species-rich vegetation, without the need to refer to individual species of presumably high aesthetic appeal (e.g. orchids) which may not always be present.

Psychologically, the increase in visual complexity with increasing species richness might explain the higher aesthetic appreciation of high-diversity communities. It has been found that a medium to high level of visual complexity of pictures is often preferred by people (Leder et al., 2004 and references therein). Similarly, humans prefer landscape scenes with moderate to high levels of complexity, measured as the number of independently perceived elements in the scene (Ulrich, 1986; Kaplan and Kaplan, 1989; Kaplan et al., 1998).

The presence of certain species explained some of the variation in the aesthetic appreciation of the experimental communities that could not be explained by their species richness. The
presence of certain herbs with brightly colored flowers like *Papaver rhoeas*, *Linaria vulgaris*, and *Leucanthemum vulgare* increased the appreciation of communities, while the presence of some grass species decreased it. Grassland management that increases the cover of grasses at the expense of forbs may thus reduce the attractiveness of vegetation. However, because only a limited number of different communities could be presented in the experiments, we cannot exclude that other species might have had significant effects on aesthetic appreciation if they had been present in more of the arrays. Other studies have also found a strong preference of humans for brightly colored flowers (Heerwagen and Orians, 1993; Lindemann-Matthies and Bose, 2007; Junge et al., 2009), and it has been suggested that such a preference may be related to the fact that bright coloring signalled food sources for people throughout evolutionary time (Heerwagen and Orians, 1993).

**Implications for conservation**

People found those communities most aesthetically pleasing that were most diverse. Our results therefore add attractiveness to humans to the list of ecosystem properties that are influenced by biodiversity and provide a further argument for its conservation. Species-rich grasslands like the ones studied are an important focus of conservation efforts in many regions, and this appears to be justified also for aesthetic reasons.

It has been suggested that there might be frequently a disjuncture between the visual aesthetic quality of landscapes and their ecological value, leading to conflicts in the setting of conservation priorities and management aims (Daniel, 2001; Gobster et al., 2007; but see Junker and Buchecker, 2008). Landscapes such as wetlands and prairies may be perceived as unattractive and people may not directly recognize their biological diversity (Gobster et al., 2007). However, the results of our study suggest that people are able to recognize diversity at
least at small spatial scales and appreciate it. In the case of European grassland vegetation the important ecological aim of high diversity and the aim of aesthetic beauty may thus be compatible.

However, in many regions of the world, intensification of management, and anthropogenic nitrogen and phosphorous enrichment are presently reducing both the species richness of grasslands and their evenness as a few species, in particular grasses, become increasingly dominant (Bobbink et al., 1998; Zechmeister et al., 2003; Stevens et al., 2004; Clark and Tilman, 2008). As the present study has shown, this is likely to reduce the aesthetic appreciation of grasslands by people and it may thus reduce the attractiveness of certain regions (e.g. the European Alps), where grasslands are a dominant feature of the landscape. This could have negative consequences for tourism. The demonstrated higher attractiveness of species-rich vegetation may thus also add an economic argument for the conservation of biodiversity in grasslands.

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References


Figure captions

Fig. 1. The relationship between mean perceived and true plant species richness. Perception of plant species richness in arrays of different diversity consisting of (a) 49 pots with plants that were presented to visitors of the Botanical Garden of the University of Marburg and the main hospital (note log-scales), and (b) 64 pots that were presented to visitors of the Botanical Garden of the University of Zurich (note log-scales). If the perceived and actual number of species were the same, all points would fall on the dotted lines. (c) Perception of plant species richness in 72 plots (2 x 2 m) in wayside meadows near Zurich by passers-by. Fitted line indicates linear regression. (d) Perception of plant species richness in 24 plots (25 x 1 m) in wayside meadows in the Alps near Davos, Switzerland, by tourists. Fitted line indicates linear regression. (e) Influence of the evenness of an array on perceived species richness. True species richness was fixed at 16 species (denoted by dotted line), but the abundance of individual species was varied to produce different levels of evenness. (f) Influence of spatial configuration on perceived species richness. True species richness was fixed at four species (denoted by dotted line), but spatial configuration was varied. Vertical bars denote ± 1 standard error.

Fig. 2. Appreciation of meadow vegetation. Five arrays of different species richness were presented simultaneously and study participants (a) in Marburg and (b) in Zurich were asked to rank them by attractiveness. Each data point is the mean appreciation of 10 - 20 people. Filled circles are the means at each level of species richness. (c) Appreciation of plots (2 x 2 m) of different species richness in wayside meadows near Zurich by passers-by, and (d) appreciation of plots (25 x 1 m) of different species richness in wayside meadows in the Alps near Davos, Switzerland, by tourists. Each plot was marked from 1 (lowest) - 6 (highest). Fitted lines indicate linear regressions. (e) Appreciation of arrays differing in evenness but
with the same number of plants species. (f) Influence of the spatial configuration of plant species in meadow arrays on people’s appreciation of the arrays. The arrays of different evenness or spatial distribution were presented simultaneously and visitors were asked to rank them by attractiveness. For a description of the arrays see legend to Fig. 1 and main text. Vertical bars denote ± 1 standard error.
Table 1 - The effect of perceived and true species richness on the appreciation of meadow arrays. The table gives the proportion of variation (i.e. of the total sums of squares, SS) in the appreciation of experimental meadow arrays and field plots explained by perceived species richness and the additional variation explained by true species richness. The data were analyzed by hierarchical general linear models in which first the effect of perceived and then that of true species richness was fitted.

<table>
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<tr>
<th>Study Type</th>
<th>Effect of Perceived Species Richness</th>
<th>Effect of True Species Richness (Fitted after Perceived Species Richness)</th>
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<td>Proportion of total SS</td>
<td>Analysis</td>
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<td>Experiment Marburg</td>
<td>76.3%</td>
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<td>37.0%</td>
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<td>(4, 8, 16, 32, 64 species)</td>
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<td>Field study Zurich</td>
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<td>$F_{1,69} = 57.1; \ p &lt; 0.001$</td>
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<td>(4 - 38 species)</td>
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<td></td>
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<tr>
<td>Field study Davos</td>
<td>2.2%</td>
<td>$F_{1,21} = 0.58; \ p = 0.45$</td>
</tr>
<tr>
<td>(15 - 53 species)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2 - The effect of the presence of individual species on aesthetic appreciation in the two experiments. Percentages of the total sums of squares in appreciation explained by the effects of the presence of individual species in the two experiments. Only species with significant effects (p < 0.05) are shown. df were 1 and 94 in all cases.

<table>
<thead>
<tr>
<th>Species</th>
<th>Proportion of total sums of squares (%)</th>
<th>p</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment Marburg</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dactylis glomerata</em></td>
<td>2.25</td>
<td>&lt; 0.01</td>
<td>negative</td>
</tr>
<tr>
<td><em>Leucanthemum vulgare</em></td>
<td>2.13</td>
<td>&lt; 0.01</td>
<td>positive</td>
</tr>
<tr>
<td><em>Bellis perennis</em></td>
<td>1.62</td>
<td>&lt; 0.05</td>
<td>positive</td>
</tr>
<tr>
<td><em>Prunella vulgaris</em></td>
<td>1.49</td>
<td>&lt; 0.05</td>
<td>negative</td>
</tr>
<tr>
<td><em>Trifolium pratensis</em></td>
<td>1.45</td>
<td>&lt; 0.05</td>
<td>positive</td>
</tr>
<tr>
<td><em>Agrostemma githago</em></td>
<td>1.21</td>
<td>&lt; 0.05</td>
<td>positive</td>
</tr>
<tr>
<td><strong>Experiment Zurich</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Papaver rhoeas</em></td>
<td>4.78</td>
<td>&lt; 0.01</td>
<td>positive</td>
</tr>
<tr>
<td><em>Linaria vulgaris</em></td>
<td>4.02</td>
<td>&lt; 0.01</td>
<td>positive</td>
</tr>
<tr>
<td><em>Festuca ovina</em></td>
<td>2.96</td>
<td>&lt; 0.01</td>
<td>negative</td>
</tr>
<tr>
<td><em>Geum urbanum</em></td>
<td>2.07</td>
<td>&lt; 0.05</td>
<td>positive</td>
</tr>
<tr>
<td><em>Poa alpina</em></td>
<td>1.89</td>
<td>&lt; 0.05</td>
<td>negative</td>
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<tr>
<td><em>Lolium perenne</em></td>
<td>1.84</td>
<td>&lt; 0.05</td>
<td>negative</td>
</tr>
<tr>
<td><em>Daucus carota</em></td>
<td>1.81</td>
<td>&lt; 0.05</td>
<td>positive</td>
</tr>
<tr>
<td><em>Tanacetum vulgare</em></td>
<td>1.72</td>
<td>&lt; 0.05</td>
<td>negative</td>
</tr>
<tr>
<td><em>Trifolium repens</em></td>
<td>1.72</td>
<td>&lt; 0.05</td>
<td>negative</td>
</tr>
</tbody>
</table>
FIGURE 1

(a) Perceived species richness vs. true species richness.
(b) Perceived species richness vs. true species richness.
(c) Perceived species richness vs. true species richness.
(d) Perceived species richness vs. true species richness.
(e) Perceived species richness vs. evenness.
(f) Perceived species richness vs. spatial distribution.

(d) (c) 
Spatial distribution

Aggregated Random Diagonal
FIGURE 2

- **FIGURE 2a**: True species richness vs. Appreciation (mean rank) for low to high levels.
- **FIGURE 2b**: True species richness vs. Appreciation (mean rank) for low to high levels.
- **FIGURE 2c**: True species richness vs. Appreciation (mean rank) for low to high levels.
- **FIGURE 2d**: True species richness vs. Appreciation (mean rank) for low to high levels.
- **FIGURE 2e**: True species richness vs. Evenness for low to high levels.
- **FIGURE 2f**: True species richness vs. Spatial distribution (Aggregated, Random, Diagonal) for low to high levels.