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Sociology of plants – a so-far untapped potential for predicting plant performance in temperate grasslands

- Helge Bruelheide, Eva Breitschwerdt, Ute Jandt, Halle an der Saale -

Abstract

Vegetation records are sources of information on the occurrence of single species, on species richness per unit area, on the abundance distribution of species in the plot and on cooccurrence of species, which can be described as sociological behavior. While the traditional Central European school of plant sociology has used co-occurrence information mainly for the purpose of classification, nature conservation and description of vegetation dynamics, the relationships to functional aspects of vegetation have been largely disregarded. It is the aim of this paper to demonstrate the importance of co-occurrence information of vegetation relevés for predicting community assembly rules. A key element of assembly rules is that species have to have certain characteristics that are reflected in their functional traits. If a plant community is assembled under strong environmental or biotic filtering, a species from the regional species pool might enter the community if it is very similar in functional trait values to the resident species of a community. In contrast, if a community is assembled under the rules of strong competitive exclusion, species are more likely to enter the community if they are most dissimilar in their traits to the resident community. As most communities can be expected to be assembled simultaneously by environmental filtering and competitive exclusion, the relative strength of environmental filtering might be predicted from the empirical probability of co-occurrence. We tested the hypotheses that additional species that most likely empirically co-occur with the resident species of a plant community show higher survival rates and better performance than those that are most similar or dissimilar in their traits to species in the resident community or randomly chosen species.

We planted 2592 plant individual of 130 different species into 54 experimental grassland plots of the German Biodiversity Exploratories that differed in land-use intensity and observed survival and growth rates of the transplants over a two-year period. The transplanted species were selected according to four different scenarios: species with highly similar or dissimilar traits to the respective resident community, based on ten different plant functional traits that were related to growth and persistance, species with the highest degree of co-occurrence to the resident species, derived from vegetation records held in the German Vegetation Reference Database using BEALS' Index, and finally, species chosen randomly from the regional grassland species pool.

As expected, the subplots into which species with highly similar or dissimilar traits to the resident community were planted showed a decrease or increase in mean trait distances, respectively, while the mean traits distances in the Beals scenario remained unchanged. Individuals of species selected by the scenario based on co-occurrence probability showed higher survival rates, and in the first year, performed better in terms of relative growth rates of leaf number as compared to species selected based on trait information or on random selection.

Our finding that introducing species with the highest degree of co-occurrence to the resident community did not change mean trait distances of this community might provide a tool to predict the relative degree of trait dissimilarity between the minimally and maximally possible dissimilarity in any given plant community without requiring any knowledge on the traits composition of the community considered. Furthermore, co-occurrence information allowed conclusions on plant survival and growth, which points to a high potential to predict individual performance from vegetation databases. The fact that plant species that are commonly found growing together also survive better if planted together provides evidence that plant communities exist and community assembly rules can be derived from co-occurrence information.

Zusammenfassung

Soziologisches Verhalten – ein bislang ungenutztes Potential zur Vorhersage von Pflanzen-Performanz in temperaten Grasländern

Pflanzensoziologische Vegetationsaufnahmen enthalten Informationen zum Vorkommen einzelner Arten, zum Artenreichtum per Fläche, zur Abundanz-Verteilung der Arten in der Aufnahmefläche sowie zum Miteinander-Vorkommen von Arten, was als soziologisches Verhalten beschrieben werden kann. Während die traditionelle mitteleuropäischen Schule der Pflanzensoziologie die Information des Miteinander-Vorkommens von Arten vor allem zum Zweck der Klassifizierung, des Naturschutzes und zur Beschreibung von Vegetationsdynamik verwendet hat, wurde der Zusammenhang mit funktionellen Aspekten der Vegetation bislang wenig beachtet. Es ist das Ziel dieses Beitrags, die Bedeutung der Co-occurrence-Information in Vegetationsaufnahmen für die Vorhersage von Regeln der Artenzusammensetzung von Pflanzengesellschaften zu zeigen. Ein Schlüssel-Element der Regeln der Gesellschafts-Zusammensetzung ist, dass Arten bestimmte Charakteristika haben müssen, die sich in ihren funktionellen Merkmalen widerspiegeln. Wenn eine Pflanzengesellschaft unter starken Filterbedingungen steht, die durch die Umwelt oder biotische Beziehungen zustande kommen, dann werden solche Arten aus dem regionalen Arten-Pool in die Gesellschaft gelangen können, die sehr ähnliche Merkmalswerte wie die vorhandenen Arten in der Gemeinschaft haben. Im Gegensatz dazu werden in Gesellschaften, die nach den Regeln des Konkurrenzausschlusses gebildet werden, eher Arten eintreten können, die in ihren Merkmalen unähnlich zu den vorhandenen Arten der Gemeinschaft sind. Da davon auszugehen ist, dass die meisten Gesellschaften gleichzeitig durch Umwelt-Filter und Konkurrenzausschluss zusammengesetzt werden, könnte die relative Stärke des Umwelt-Filters von der empirischen Wahrscheinlichkeit des Miteinander-Vorkommens vorhergesagt werden. Wir haben die Hypothesen getestet, dass weitere Arten, die mit hoher Wahrscheinlichkeit mit den vorhandenen Arten in einer Pflanzengesellschaft vorkommen, höhere Überlebensraten und eine höhere Performanz zeigen als Arten, die in ihren Merkmalen besonders ähnlich oder unähnlich zu den vorhandenen Arten sind oder als solche, die zufällig ausgewählt werden.

Insgesamt haben wir 2592 Pflanzenindividuen von 130 verschiedenen Arten in 54 verschiedene Grünland-Flächen der Deutschen Biodiversitäts-Exploratorien gepflanzt und ihr Überleben und ihre Wachstumsraten über zwei Jahre beobachtet. Die eingepflanzten Arten wurden nach vier verschiedenen Szenarien ausgewählt: Arten mit sehr ähnlichen oder sehr unähnlichen Merkmalen zu den vorhandenen Arten in der jeweiligen Gesellschaft, basierend auf zehn verschiedenen funktionellen Merkmalen, die mit Wachstum und Persistenz in Zusammenhang stehen, Arten mit dem höchsten Maß an Co-occurrence-Wahrscheinlichkeit mit den vorhandenen Arten, die mittels BEALS' Index aus der Deutschen Vegetations-Referenz-Datenbank ermittelt wurde, sowie schließlich Arten, die zufällig aus dem regionalen Grünland-Arten-Pool ausgewählt wurden. Wie erwartet, zeigten die Teilflächen, in die Arten mit sehr ähnlichen oder unähnlichen Arten in Bezug zu den vorhanden Arten gepflanzt wurden, eine Abnahme bzw. Zunahme an mittleren Merkmals-Distanzen, während die mittleren Merkmals-Distanzen im Beals-Szenario unverändert blieben. Individuen von Arten, die auf der Basis von Co-occurrence-Wahrscheinlichkeit ausgewählt wurden, zeigten höhere Überlebensraten und im ersten Jahr eine höhere Performanz in Bezug auf die relative Wachstumsraten der Blattzahl im Vergleich zu Arten, die Merkmals-basiert oder zufällig ausgewählt wurden.

Unser Befund, dass sich die mittleren Merkmals-Distanzen der Gemeinschaft nicht geändert haben, wenn Arten mit hoher Wahrscheinlichkeit des Miteinander-Vorkommens in die Gemeinschaft eingebracht wurden, könnte eine Methode darstellen, den relativen Grad der Merkmals-Unähnlichkeit zwischen der minimal und maximal möglichen Unähnlichkeit in jeder beliebigen Pflanzengesellschaft vorherzusagen, ohne die Merkmals-Zusammensetzung der Gemeinschaft kennen zu müssen. Desweiteren, erlaubt die Co-occurrence-Wahrscheinlichkeit Rückschlüsse auf Überleben und Wachstum, was auf ein hohes Potential hinweist, Pflanzen-Performanz aus Vegetations-Datenbanken vorherzusagen. Die Tatsache, dass Pflanzenarten, die häufig zusammen vorkommen auch besser überleben, stellt auch einen Beweis dafür dar, dass Pflanzengesellschaften existieren und dass Regeln der Gesellschafts-Zusammensetzung aus der Co-occurrence-Wahrscheinlichkeit abgeleitet werden können.

1. Introduction

Vegetation records have a long tradition in European plant sociology (BRAUN-BLANQUET 1915). Basically, they capture both presence and relative amount of all species in a plot. Typically, vegetation is stratified into height layers representing the vertical structure, such as trees, shrubs, herbs & forbs and cryptogams. Within these layers, the relative amount of each species is estimated as per cent cover, number of individuals, or a combination of both (BECKING 1957, BRAUN-BLANQUET 1964, WESTHOFF & VAN DER MAAREL 1978, KNAPP 1984). To compile a complete list of all vascular plants in a plot requires considerable skill which probably has inspired many botanists to become masters of this discipline (Fig. 1). Such vegetation records have been collected for more than a century, covering all types of vegetation and locations, and since several decades many attempts have been made to compile them in databases



Figure 1: Reinhold Tüxen taking a vegetation record on the Campinos heathlands on the IAVS Poland excursion in 1963. Photograph by Ernst-Gerhard Mahn.

(EWALD 2001, SCHAMINÉE et al. 2009). The Global Index of Vegetation Plot Databases (GIVD) lists 3,595,774 plots that were registered by June 2015 (www.givd.info). However, estimates for the total amount of available relevés might be several times that much. Recent initiatives have compiled a considerable amount of relevés for Europe (European Vegetation Archive, CHYTRÝ et al. 2015) or worldwide (sPlot, DENGLER et al. 2014). The amount of vegetation data is tremendous. The recent sPlot 2.0 database version, a synthesis project of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, has captured 1.1 mio. forest and grassland plots from more than 100 national and continental databases and covers more than 100 countries. This corresponds to 24.3 mio entries of species occurrences with geographical coordinates. As with information from floristic (Atlas Florae Europaeae, http://eeb.lu.lv/grozs/BotanikasEkologijas/Flora_Europa/www/www.helsinki.fi/kmus/ afe.html) and biodiversity databases (Global Biodiversity Information Facility, GBIF, www.gbif.org), these data allow to compile global distribution maps (e.g. WELK & BRUEL-HEIDE 2006) and to construct species distribution models (SDMs, e.g. GUISAN & ZIMMER-MANN 2000, GUISAN & THUILLER 2005) and to derive a species realized niche (e.g. HOF-MANN et al. 2013). A second field making use of these data are biodiversity calculations, ranging from estimates of α diversity (WILSON et al. 2013) to global estimates (WHITTAKER et al. 2001, MCGLINN et al. 2015). The third type of information in relevés is relative amount, which is required to weight the contribution of the plant species in the plot to ecosystem functions, when calculating community weighted means (e.g. GARNIER et al. 2004, EICHEN-BERG et al. 2014) or functional diversity (e.g. BÖHNKE et al. 2014; KRÖBER et al. 2015). The fourth information component in vegetation plots is co-occurrence information, on which we focus in this paper.

Co-occurrence information is the basis for most of the declared scientific aims of plant sociology, such as in the sequence of their importance in 20th century German plant sociology providing vegetation classification systems, defining plant communities as a basis for conservation, describing vegetation dynamics and understanding community assembly rules (DIER-SCHKE 1985, 1994, CHASE 2003). However, in all four research fields there are increasing



Figure 2: Literature review in the Villa databases, hosted by the group of vegetation analysis and compiled by Hartmut Dierschke and run on the Faust 2.0 platform (Doris Land, Oberasbach, Germany). Articles were retrieved by the making use of the hierarchical thesaurus and counted by year. Classification: down "Pflanzensoziologisches System" (n=5759 references in total), Conservation: down "Naturschutz" (n=3024), Dynamics: down "Dynamik" (including "Fluktuation", "Sukzession") (n=656) and Community assembly: down "biogene Wechselwirkungen" or down "experimentelle Vegetationskunde" (n=302). There were no entries for "Trait" or "Merkmal" in the Villa database.

numbers of publications with time (Fig. 2). In contrast, internationally the focus has been quite different, as seen in the review of these topics in the Web of Science (Fig. 3). Here, most studies were undertaken in the field of vegetation conservation and dynamics. Since 2000, research on functional traits and community assembly received increasing attention. Most remarkably and in contrast to the European focus, vegetation classification has not only received much less attention in international literature, but also does not follow the general trend of increasing publication numbers (Fig. 3). The comparison of these two reviews shows that Central European plant sociology had a very different focus with only little attention to the co-occurrence information captured in relevés for functional research. It is the aim of this paper to demonstrate that relevés that might have been made for a different purpose, such as for classifying vegetation or describing vegetation dynamics, can serve to predict community assembly rules.



Figure 3: Literature review in the Web of Science (apps.webofknowledge.com, accessed 25.04.2015). Articles were retrieved by the using the following search terms and counted by year. Conservation: "vegetation" and (("conservation*") or ("planning")) (n=17347 references in total), Dynamics: ("vegetation" or "plant") and (("succession*") or ("vegetation dynamic*")) (n=17473), Functional traits: (("vegetation" or "plant") and "functional" and "trait*") (n=6210), Community assembly: ("vegetation" or "plant") and "community assembly" (n=838), Classification: ("vegetation classification" or "vegetation *taxonom*") (n=641). The lines were obtained by a general additive model (gam), using a loess smoothing parameter of 0.5.

Assembly rules can involve very different explanations for coexistence of species (LEI-BOLD et al. 2004), but a key element is the idea of different filters that determine which species from the local species pool can pass into the local community, establish themselves and persist in these communities (LORTIE 2004, WEIHER et al. 2011). In order to pass a certain filter, species have to have certain characteristics which are assumed to be reflected in their functional traits (WILSON 2007; ORDOÑEZ et al. 2009). If a community is assembled exclusively under strong environmental or biotic filtering, successful candidates from the regional species pool will be those that are the most similar species in their traits to the species in the resident community (Sim scenario, Fig. 4C). In contrast, if a community is assembled under the rules of strong competitive exclusion, immigrants should be more successful if they are most dissimilar in their traits to the resident community (MACARTHUR & LEVINS 1967, Dissim scenario, Fig. 4D). However, most communities can be expected to be assembled simultaneously by environmental filtering and competitive exclusion. The degree of environmental filtering will depend on the strength of the filter. In German grassland communities, in many cases the

strongest filter is land use (LALIBERTÉ et al. 2010), ranging from annual mowing or lowintensive grazing to frequent mowing and grazing (BLÜTHGEN et al. 2012). We made use of the gradient in land use intensity of the German Biodiversity Exploratories (FISCHER et al. 2010), to sample communities that differ in strength of environmental filtering. The direct impact of land use on assembly processes has been analyzed in detail by BREITSCHWERDT et al. (2014; 2015). Here, we focus on the predictive power of co-occurrence information for community assembly, and take land use only as an environmental factor that creates commu-nities varying in assembly processes. We suggest that for an unknown strength of the environ-mental filter, the degree of similarity or dissimilarity of the traits a species should have to become established in a given community might be derived from the empirical probability of co-occurrence of this species with the resident species. To obtain the required co-occurrence information we made use of a large collection of vegetation relevés, produced by phytosociologists over decades. We used the German Vegetation Reference Database (GVRD, JANDT & BRUELHEIDE 2012) and calculated BEALS (1984) index. Without making assumptions on the species characteristics, as required in trait-based approaches in community assembly approaches (WILSON 2007), bringing species with the highest probability of co-occurrence to the resident species into the community and monitoring their survival and performance should answer the question whether filtering or competitive exclusion is the more important community assembly process (Beals scenario, Fig. 4A). Finally, there is the possibility that the community is assembled randomly from the regional species pool (Random scenario, Fig. 4B).



Figure 4: Scheme of the four different scenarios employed by BREITSCHWERDT et al. (2014) to test community assembly rules. These scenarios were tested by adding different species of a regional species pool to existing communities. The species were selected according to: (A) Highest probability of co-occurrence (Beals scenario), (B) Randomly chosen species (Random scenario), (C) Increase of mean trait distance by adding most dissimilar species (Dissim Scenario) and (D) Decrease of mean trait distance by adding most similar species (Sim Scenario). It was expected that species selected by the Dissim scenario perform better under strong environmental filtering, whereas species selected by the Sim scenario perform better when complementarity processes prevail.

We here specifically ask whether this empirical co-occurrence information on potential new colonizing species can predict the degree of their trait similarity or dissimilarity to the resident community, and whether the species with the highest degree of co-occurrence probability to the resident community perform better than species that are most similar or dissimilar in traits to the resident species. In particular, we hypothesized, (i) that the mean trait distances of the plant community change positively and negatively through adding species according to the Sim and Dissim scenario, respectively, while the change in mean trait distances of the Beals scenario takes an intermediate position; (ii) that the additional species that most likely empirically co-occur with the resident species show higher survival rates than those that are most similar or dissimilar in their traits to those in the resident community or randomly chosen species. Finally, we tested the hypothesis that (iii) the species in the Beals scenario perform better than those of the other scenarios, i.e. show the highest growth rates.

2. Materials and methods

The study was conducted in the experimental grassland plots of the German Biodiversity Exploratories (FISCHER et al. 2010). We selected 18 plots each in the three study regions (Schwäbische Alb, South Germany; Hainich, Central Germany and Schorfheide, Northeast Germany). Land use type (meadow, pasture, mown pasture) and land use intensity differed among plots. In each of the 54 plots, we established eight 1 x 1 m-subplots and planted six individuals of different species into every subplot, resulting in a total of 2592 added plants. The species were selected from a total pool of 130 species according to the four transplant addition scenarios (Sim, Dissim, Beals and Random, see Fig. 4). Species in the Sim and Dissim scenarios were selected in way to have the lowest and highest mean pairwise trait distance to the resident species in the plot, respectively, based on the following traits: SLA, LDMC, height, leaf anatomy, leaf persistence, leaf distribution, vegetative reproduction, clonal growth organs, lateral spread, physical defense. In the Beals scenario, those species were planted that had the highest probability to co-occur with the resident species in the German Vegetation Reference Database (GVRD, JANDT & BRUELHEIDE 2012). We selected those species that ranked highest in BEALS (1984) index (1):

(1)
$$p_{pi} = \frac{1}{N_p} \sum_{j}^{N_p} \frac{M_{ij}}{M_j}$$

The probability p_{pi} for species *i* to occur in a relevé *p* is calculated from joint occurrences M_{ij} in the GVRD to all species *j* of the total number of species in that plot N_p , divided by the number of plots M_j in which the species *j* is present in the GVRD. Finally, in the Random scenario, the species were selected randomly from the species pool. Further information of the experimental design and the scenarios can be found in BREITSCHWERDT et al. (2014). After being planted in April 2012, the transplants were monitored regularly for growth and survival in 2012 in April, May, July, August and October and in 2013 in May, June/July and September. These eight monitoring events were numbered from zero to seven. Here, we only present survival rates until the end of the vegetation periods 2012 and 2013 (i.e. at monitoring dates 4 and 7, respectively) and relative growth rates (RGR) of number of leaves in the vegetation periods 2012 and 2013 (i.e. defined by monitoring dates 1 to 4 and 5 to 7, respectively). RGR was calculated according to HUNT & CORNELISSEN (1997).

Data analysis

In a first step, we tested whether the randomly chosen subplots differed in trait dissimilarity before we added additional plant individuals of further species. We calculated pairwis trait \overline{d} distances between all species in every subplot according to formula (2).

(2)
$$\vec{d} = \frac{\sum_{i=1}^{N} \sum_{j=1}^{N} d_{ij}}{N \cdot N}$$

where d_{ij} is Gower's distance calculated across all ten traits, irrespective of their scale (i.e. nominal, or ratio, PAVOINE et al. 2009) and N is the number of species in a subplot. In a seond

step, we calculated \overline{d} across all species in the subplot including the six selected species planted into the subplots according to the different scenarios. Survival rates were calculated as the mean of the six species planted into one subplot until the end of the first and second vegetation period. Differences between the four scenarios in mean trait distances as well as survival rates were calculated with mixed linear models in R (lme, package nlme), using Exploratory (Schwäbische Alb, Hainich or Schorfheide) and plot nested in Exploratory as random factors. Differences between scenarios were tested with Tukey post-hoc tests using the glht command from the multcomp package (HOTHORN et al. 2008).

Differences in RGRs between scenarios were based on the single individuals and also tested with mixed linear models in R (lmer, package lmerTest, KUZNETSOVA et al. 2013) using exploratory (Schwäbische Alb, Hainich and Schorfheide), plot nested in exploratory, subplot nested in plot and species identity as random factors. Including species as crossed random factor accounted for species-specific differences in RGRs. For all statistical analyses, we used the software R version 3.0.2. (R CORE TEAM 2013).

3. Results

No significant differences between the four scenarios were encountered before the experiment (Fig. 5A), demonstrating that the trait composition between subplots did not differ before additional species were planted into the subplots. After planting six additional species into the subplots, the mean trait distances across all ten traits differed between the four scenarios. As expected, the species planted into the Dissim and Sim subplots resulted in an increase and



Figure 5: Mean pairwise trait distances of all species in the community of the four scenarios (Beals, Dissim, Random and Sim) A) before planting six individual of different species and B) the change in distances after planting the additional species in April 2012. Values are multi-trait distances and based on ten traits. Boxes show quartiles and medians across all 54 plots and two subplots per plot (n = 108 per scenario). Whiskers show 1.5 times the interquartile ranges. ANOVA for scenario A) p=0.9775, B) p<0.0001. Small letters indicate statistically significant differences among the scenarios according to a Tukey post-hoc test.

decrease, respectively, with a change of 0.052 and 0.017 in mean trait distances (Fig. 5B). The Random scenario ranked exactly between Dissim and Sim with a change in overall mean trait distance of 0.022. In contrast, the mean traits distances in the Beals scenario changed only by 0.004, which was not significantly different from 0. For further statistical details see Table 2 in BREITSCHWERDT et al. (2014).

Survival rates of the transplants after one vegetation period differed between the four scenarios, and were highest and lowest in the Beals and Dissim scenario, respectively (Fig. 6A). After another year in the field, survival rates continued to decrease but remained similarly dif-



Figure 6: Survival rates of the species planted into the community according to the four scenarios (Beals, Dissim, Random and Sim) A) after the first vegetation period in 2012 (at monitoring date 4) and B) in the second vegetation period 2013 (at monitoring date 7). Values are averages across the six individuals planted per subplot. For statistical details see BREITSCHWERDT et al. 2014). Boxes show quartiles and medians across all 54 plots and two subplots per plot (n = 108 per scenario). Whiskers show 1.5 times the interquartile ranges. ANOVA for scenario A) p<0.0001, B) p<0.0001. Small letters indicate statistically significant differences among the scenarios according to a Tukey post-hoc test.

ferent between the scenarios (Fig. 6B).

Relative growth rates of leaf number did not reflect the survival rates and owing to a large variation between positive and negative values of RGR showed a much less clear pattern (Fig. 7). For the first vegetation period, RGR of leaf number was highest for plants in the Beals scenario and lowest in lowest in the random scenario (Fig. 7A). In the second vegetation period, growth rates were no longer statistically different from each other (Fig. 7B). For differences in RGR on other response variables and in final biomass harvest see BREITSCHWERDT et al. (2015).

4. Discussion

Our findings supported the first hypothesis that species added to the subplots in the Beals scenario resulted in a change in mean trait distances that ranked between the changes observed in the Sim and Dissim scenarios. An unexpected result was that adding species according to the Beals scenario did not result in any significant change in mean pairwise trait distances as compared to the resident community without added species. This means that the



Figure 7: Relative growth rates of the species planted into the community according to the four scenarios (Beals, Dissim, Random and Sim) A) in the first vegetation period (monitoring dates 1-4) and B) in the second vegetation period (monitoring dates 5-7). For statistical details see BRE-ITSCHWERDT et al. 2015). Boxes show quartiles and medians across all 54 plots and two subplots per plot (n = 108 per scenario). Whiskers show 1.5 times the interquartile ranges. ANOVA for scenario A) p=0.0321, B) p=0.0001. Small letters indicate statistically significant differences among the scenarios according to a Tukey post-hoc test.

species added had on average the same distances in trait values to the resident species as the resident species had among themselves. Taking the change caused by planting the six species in the Sim and Dissim scenario as extremes (i.e. -0.017 and +0.052, respectively), the Beals scenario (+0.004) ranked at 30% between Sim and Dissim, being closer to the Sim than to the Dissim scenario. Thus, species with the highest degree of co-occurrence to the resident community tended to be 30% similar and 70% dissimilar, respectively, with respect to maximal similarity and dissimilarity in traits of all species available in the species pool. As this degree was encountered across different intensity of environmental filtering, it might be constant across all grassland communities in our study. If this should be confirmed by future studies, the co-occurrence information used in the Beals index might provide a tool to predict the degree of trait dissimilarity between the minimally and maximally possible dissimilarity in any given community without requiring any knowledge on the traits composition of th community considered. Thus, co-occurrence information as used in Beals index might inform community assembly models, a so-far untapped role of vegetation relevés in science.

We also can confirm our second hypothesis that the species with a high probability of cooccurrence with the resident species show higher survival rates than species selected by the other scenarios. This means that those species in the resident community that co-occur with the same species elsewhere in the database also have a high chance to survive in that particular community. These findings from our experiment would confirm the early assumption of plant sociologists that communities are not random assemblies but to a certain degree defined (e.g. NOY-MEIR & VAN DER MAAREL 1986, VAN DER MAAREL 1996). The fact that species that are commonly found growing together also survive better if planted together shows that they are either adapted to the same environmental filter, in our case land use, or are able to cope with each other, and thus fit into the network of positive and negative interactions that exist in that community. In this aspect our experiment provides evidence that communities exist and community assembly rules can be derived from co-occurrence information. In combination with the result of an optimal degree of trait dissimilarity in the Beals scenario, we now might conclude which trait combination might result in highest survival of new colonizers in a given community. Using co-occurrence information in this way would allow to predict all types of phenomena plant sociologists have been intrigued since decades, such as predicting succession series (SMITH et al. 2001, JOHNSOn & MIYANISHI 2008) or plant invasions (e.g. GALLIEN et a. 2014).

Finally, we also demonstrated that plants in the Beals scenario had higher RGR of leaf numbers than those in the other scenarios, which however was only encountered in the first vegetation period and disappeared in the second. Thus, we can only partly confirm the third hypothesis. This discrepancy to the observed survival rates might be explained by different facts. First, we exposed our transplants to the ambient land use, which interfered with RGR measurements and also explains observed negative values in RGR that occurred after mowing or grazing. Second, high growth rates might not always the best strategy to survive. This is easily demonstrated by the well-known growth-persistence trade-off, which defines the different strategies of stress tolerators versus competitors in GRIME's (1979) CSR scheme but is also evident in key functional traits such as in the leaf economics spectrum (WRIGHT et al. 2004) that describes the different leaf strategies of quick or slow return on investments of nutrients and dry mass. Third, BREITSCHWERDT et al. (2015) have shown that the scenario was only important in isolation but showed strong interactions with land use intensity and the functional diversity of traits and functional identity (expressed as community weighted means of traits), which differed between the different observation intervals. For example, land use intensity had a positive effect on height growth in winter and a positive one in the subsequent summer interval. Fourth, growth rates can only be measured on individuals that survive, which applies to all scenarios. Thus, elimination of plants that did not fit into the community and the prevailing land use would finally result in a selection of plants that all share similar growth characteristics, irrespective of the scenario by which they had been initially selected. This explains the disappearance of any differences in growth rates with the ongoing experiment. It also shows the limitations of experiments such as ours because single plants have limited life spans and the ultimate success of colonization can only be judged if the long-term demography is known (EBENHARD 1991). However, co-occurrence information might also be useful for predicting long-term population dynamics, as has been demonstrated by MILDÉN et al. (2006) who predicted the suitability of habitats for growth of Succisa pratensis in Swedish grasslands. Sowing seeds of Succisa pratensis into different habitats they found a strong significant positive relationship between Beals index and seedling germination and survival.

In summary, our findings clearly demonstrate the high potential of co-occurrence information on predicting trait combinations of communities and survival of colonizers, and with some reservations on predicting growth rates of individual plants. Although the pioneers of plant sociology did not foresee that the co-occurrence information captured in relevés might serve these purposes, their thinking often built on personal experience of having seen plant species in a vast amount of different contexts, which allowed guesses on that species' behaviour in a particular community. Although plant sociology was not able to operationalize this knowledge, the data it left behind now forms the basis for this type of new analysis. Making use of vegetation relevés in this way requires to make them accessible in large databases, which underscores the effort that has been put into establishing vegetation databases all around the world (DENGLER et al. 2011, 2014, JANSEN et al. 2012). It is amazing that these data have mainly been considered useful for refining vegetation classification systems (BRU-ELHEIDE 2000), for providing nature conservation data (DIERSSEN et al. 1999), and more recently, for combining the relative abundance data of the plots with traits (WEBB et al. 2010) or phylogeny (e.g. MAYFIELD & LEVINE 2010) to advance functional community theory. However useful these approaches are, they have so far overlooked the predictive power behind the sheer mass of plots that have become available. These data may not only have the potential to predict the outcome of assembly rules such as survival and growth rates but also the type of interactions such as complementarity, facilitation and competition. Accomplishing this will require further experiments but also new forms of synthesis approaches which so far have not made use of the co-occurrence information in relevés. As a consequence, the recently emerging trend in increasing publication numbers on community assembly (Fig. 3) can be expected to increase in the next decades.

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Authors address:

Helge Bruelheide, Eva Breitschwerdt, Ute Jandt

1: Martin Luther University Halle Wittenberg, Institute of Biology / Geobotany and Botanical Garden, Am Kirchtor 1, 06108 Halle, Germany

2: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig.

E-mail: helge.bruelheide@botanik.uni-halle.de, eva.breitschwerdt@botanik.uni-halle.de ute.jandt@botanik.uni-halle.de

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