# ID (set by BEO)

# Date

22.03.2016

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# Title

Is there ecosystem-level synchrony in functional trait distribution across trophic guilds?

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We will adhere to the authorship criteria of the BE and everyone who contributes data to the analysis will be offered authorship.

# Rationale

Species traits within trophic guilds are highly correlated amongst each other, with the consequence that certain trait combinations (i.e., ‘functional strategies’) are repeatedly observed in nature. In multi-dimensional trait space, variation can often be reduced to just a few principal components. For example, in plants, much trait variation can be explained by the ‘plant economics spectrum’: a single axis differentiating between conservative and exploitative resource use and reproductive strategies (Reich 2014; Díaz et al. 2016, Salguero-Gómez et al. 2016).

Functional strategies reflect adaptation to environmental conditions (Lavorel et al. 2011; de Vries et al. 2012; Reich 2014). For instance, community-level specific leaf area (SLA) responds to environmental drivers by declining with drought and increasing with nutrient enrichment (de Vries et al. 2012; Reich 2014). Similarly, the loss of functional trait diversity can occur where niche space is constricted, e.g. due to grazing, mowing or fertilization (Flynn et al. 2009, Harpole et al. 2012, Birkhofer et al. 2015). Functional strategies are also related to the specificity and strength of interactions of a species with other species or trophic groups, e.g. a (Eklöf et al. 2013; Kunstler et al. 2016). To date, most evidence for such synchronous shifts of species traits has been drawn from observations at two adjacent trophic levels (e.g. plants and herbivores, Moretti et al. 2013; predators and prey, Brose et al 2006;). and systematic shifts in trait distribution have been found to bridge multiple trophic guilds (Flynn et al. 2009; Eklöf et al. 2013), driven by either species interactions or by shared environmental responses.

It is thus possible that the constraints of the plant economics spectrum extend across multiple trophic guilds, e.g. by the quality of plant tissue affecting the trait distribution of both above and belowground consumer communities, and of their respective predators. This would be reflected by a correlation between the trait distributions of the trophic guilds within an ecological community. This synchrony of trophic-guild trait spaces within communities along few principal-component axes can be interpreted as whole ecosystem-level functional spectra, which could potentially lead to the identification of general ecosystem functional types, e.g. low-vs.-high turnover systems, with the respective traits observed across multiple trophic guilds.



***Fig. 1*** *– a) Collapsing n-dimensional trait distribution of trophic guilds across plots to principal components will reduce complexity of trait data to the ecosystem-level functional strategy axis and allows correlating them to environmental drivers, such as land use intensity. b) Testing alternative path models of correlation will inform about the causal relationship between functional strategies across trophic guilds.*

Based on this knowledge, we hypothesize that the community weighted means of functional traits will be synchronized across multiple trophic levels in the Biodiversity Exploratory grasslands. Specifically, we hypothesize that an increase in land-use intensity will shift plants towards an exploitative strategy, aboveground invertebrates of primary and secondary consumer groups towards generalist strategies (e.g. Simons et al. 2015b), and microbes towards fast-growing bacterial dominance (see notes for further detail). We further hypothesize that the strength of trait synchrony across functional groups is sensitive to changes in land-use intensity. Functional trait variation across multiple trophic levels is found to be reduced by intensification of land use (Gámez-Virués et al. 2015), mainly due to the loss of rare, specialist trait values. Therefore, given the homogeneity of traits in generalist communities, the synchrony of trait distribution across trophic guilds may be diminished in high land use intensity sites. This also might indicate the loss of ecosystem resilience (see notes for further detail).

Clusters in ecosystem-level trait distribution could potentially be associated with certain rates and types of ecosystem processes (de Bello et al. 2010, Lavorel and Grigulis 2012). Thus, if trait synchrony across trophic guilds holds true, this may also provide an approach to relate ecosystem-level functional spectra of traits to the provision of ecosystem services (e.g. via the values of whole ecosystem PCA axes). Such relationships will be investigated if ecosystem level functional spectra are identified, and we will also explore relationships between the trait distributions (functional diversity) of multiple trophic levels.

# Methods

## Principal component analysis

Within each trophic guild, trait data will be coerced to plot-level community weighted means (CWM). Of these, a matrix of traits (columns) per plot (rows) will be fed into a principal component analysis to identify significant axes within each trophic guild (Fig. 1a). The vectors on the first and second principal component axes will serve as the response values for the further steps of the analysis.

As a complement to CWM, other community level metrics of functional diversity (e.g. Rao's Q, Petchey and Gaston 2006) will be applied to account for complementarity and redundancy of traits within communities. Additional metrics for the variation of trait values within each plot will be calculated (variance, skewness, multimodality) and undergo the same procedure as the CWM values.

## Correlation and structural equation modeling

To correlate the vectors of multiple trophic levels, we will apply path analysis on the principal component data we received from the previous steps (Fig. 1b). Multiple pathway possibilities for causal correlations between the principal-component data of the trophic groups (response) and the indicators of land use (explanatories) will be explored and compared via goodness-of-fit metrics.

This will give us a mathematical estimate of the relatedness of adjacent trophic guilds and whether they are driven by interactions or a shared response to land use.

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# Data requirements

We plan to focus on the grassland plot data of the Biodiversity Exploratories, because trait data are more complete and due to the expertise of the group involved. Future work may extend to forest ecosystems.

## Species trait data per trophic guild

We require data on species traits for multiple functional groups of the above and below ground ecosystem compartment. At minimum we would like to include plants, herbivores, predators, and soil microbial community. These data have already been compiled by Gossner et al (2015). Further functional groups could easily be included if data are available (e.g. parasitoids, root feeders, pollinators).

## Plot-level species abundance data (over time)

The plot-level assessments of species abundances (Simons et al. 2014, 2015a, 2015b) will be used to compile community weighted means, variances and skewness metrics of traits per trophic guild for each plot at each point in time.

## Plot-level data of land-use intensity factors

The standard plot data of the Biodiversity Exploratories provide information on grazing, mowing and fertilization frequencies, compiled into the Land Use Index (LUI). We will explore which of those factors, or their combination, best predicts the synchrony of changes in trait distribution.

# Notes

## Evidence for trait synchrony across trophic guilds

Arthropod herbivore specialization depends on the relative nitrogen content of foliage (Mattson 1980), which relates to the plant economic spectrum (Díaz et al. 2016). The same is true for pollinators, which specialize on particular plant traits including phenology, flower height and shape (Junker et al. 2013). For instance, butterfly life-history traits span along an axis of body-size and reproduction cycles ('voltinism') that is highly correlated to the size of host plants (Bartonova et al. 2014). Further, the body mass of predators is typically one or two orders of magnitude above the body mass of their prey (Brose et al. 2006; Hatton et al. 2015), which is due to the allometric constraints of feeding and metabolism, a fact that directly relates to the energy use and production of whole populations and communities (Ehnes et al. 2014; Hatton et al. 2015). Such associations also extend belowground where bacterial-dominated microbial communities with fast turnover rates are associated with plant communities dominated by exploitative species with rapid turnover and high quality litters, and slow, fungal dominated communities with conservative plants (Wardle 2002; de Vries et al. 2012).

## Trait-space responses to land use change

Trait variation of plants is expected to be reduced by land-use intensification due to the selection of fast-growing, highly competitive plants, and the loss of specialists (Allan et al. 2015). This propagates to arthropod communities, which also lose specialists and their characteristic traits where land-use intensity increases (Weiner et al. 2011, 2014; Simons et al. 2015*b*; Mangels et al., in preparation). The remaining generalists are expected to have a higher overlap in their functional traits. As diversity in terms of species number and function is reduced, the trait spectra of communities thus become simpler. This likely will be reflected in stronger synchrony of the community’s trait spaces at high degrees of disturbance by grazing, mowing and fertilization.

## Perspectives

By describing correlations in trait-space across functional groups we get a general understanding − i.e., irrespective of the particular species identities involved − of how multiple functional guilds respond to each other and to environmental change in the wider ecosystem context.

Functional trait diversity has been identified to be a better predictor of ecosystem function and services than species richness alone (de Bello et al. 2010). Therefore, we propose to relate the functional spectra of ecosystems along environmental gradients to the levels of ecosystem function and services observed. Also, the knowledge of relations between multi-trophic trait spaces might be used to advance food-web models that distribute species of trophic guilds along the identified virtual niche axes (i.e. the principal-component axes) and to simulate the relationship between multi-trophic biodiversity and ecosystem function with high realism.