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# Working title:

Is there whole ecosystem level synchrony in functional trait distribution?

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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.

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# Rationale

Species traits within trophic guilds are highly correlated amongst each other, with the consequence that certain trait combinations (functional strategies) are repeatedly observed in nature. In multi-dimensional space, trait 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 growth strategies (Reich 2014; Díaz et al. 2016; Salguero-Gómez et al. 2016). Functional strategies reflect adaptation to environmental conditions. The diversity and distribution of strategies within a community can therefore often be seen to co-vary along environmental gradients (Lavorel et al. 2011; de Vries et al. 2012). For instance community-level specific leaf area (SLA) responds negatively to drought and positively to nutrient availability (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 (Harpole et al 2012, REF Exploratories).

There is evidence that in response to environmental change systematic shifts in traits occur across multiple trophic guilds. This could be driven by either species interactions (trophic or non-trophic), or by shared environmental responses. To date, evidence for such shifts has been drawn mostly from observations at two adjacent trophic levels, where it is seen that traits in one trophic guild correlate with traits in a directly interacting trophic guild (e.g. plants and herbivores, predators and prey).

If the constraints on economics extend across multiple trophic guilds, e.g. by the quality of plant tissue affecting both above and belowground communities, this would be reflected by a correlation in the trait distribution in multi-dimensional trait space. Accordingly, this variability could be reduced to a few principal-component axes describing whole ecosystem level functional axes, much in the same way that multiple species level traits can be categorized into functional strategies (Díaz et al. 2016).

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 small body sizes (e.g. Simons et al. 2016), and microbes towards bacterial dominance. Furthermore, trait variation is reduced by intensification of land use (Gámez-Virués et al. 2015). We hypothesize that the strength of trait synchrony across functional groups is sensitive to changes in land-use intensity.

If trait synchrony across trophic levels holds true, this also provides a new approach to relate trait variation to the provision of ecosystem services (Lavorel and Grigulis 2012). Community-wide shifts in trait diversity may be propagated to the ecosystem level could potentially explain variation in ecosystem multi-functionality (Soliveres et al. in preparation). Such relationships will be investigated if ecosystem level trait axes are identified, and we will also explore relationships between the trait distribution (functional diversity) of multiple trophic levels.

# Analysis

## Principal component analysis

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

Besides community weighted means of traits, other community level metrics of functional diversity (e.g. Rao's Q, Petchey and Gaston 2006) will be applied to identify complementarity and redundancy within communities.  
Additionally, metrics for variation within each plot will be explored (variance, skewness, multimodality) and undergo the same procedure.



**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 to correlate 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.

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## 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 AIC.

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.

# 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 ... . 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 will be used to compile community weighted means, variances and skewness metrics of 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.

# Further notes

## Evidence for trait synchrony

Arthropod herbivore specialisation 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 specialise 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 fast turnover bacterial dominated microbial communities are associated with plant communities dominated by exploitative species 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. This propagates to arthropod species, who also lose specialists under intensive land use (e.g. nocturnal moths, Mangels et al., in preparation). We expect this to result in less correlation in trait diversity 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 in the wider ecosystem context and how environmental changes propagate to ecosystem function and services. Such knowledge might be used to inform a new class of food-web models that distribute species of trophic guilds along the identified principal-component axes and, while being simple, can be applied to simulate the relationship between multi-trophic biodiversity and ecosystem function with high realism.

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