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Title: Trait-matching and mass effect determine the functional response of herbivore communities to land use intensification

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Summary

1. Trait-based approaches represent a promising way to understand how trophic interactions shape animal communities. The approach relies on the identification of the traits that mediate the linkages between adjacent trophic levels, i.e. “trait-matching”. Yet, how trait-matching explains the abundance and diversity of animal communities has been barely explored. This question may be particularly critical in the context of land use intensification, currently threatening biodiversity and associated ecosystem services.
2. We collected a large dataset on plant and grasshopper traits from communities living in 204 grasslands, in an intensively managed agricultural landscape. We used a multi-trait approach to quantify the relative contributions of trait-matching and land use intensification acting at both local and landscape scales on grasshopper functional diversity. We considered two key independent functional traits: incisor strength and body size of grasshopper species. Incisor strength, a resource-acquisition trait, strongly matches grasshopper feeding niche. Body size correlates with mobility traits, and may determine grasshopper dispersal abilities.

3. Plant functional diversity positively impacted the diversity of grasshopper resource-acquisition traits, according to the degree of trait-matching observed between plants and herbivores. However, this positive effect was significantly higher in old grasslands. In addition, the presence of specific habitats in the landscape (i.e. wood and alfalfa) strongly enhanced grasshopper resource-acquisition trait diversity in the focal grassland. Finally, grasshopper body size increased with landscape simplification, although the response was modulated by local factors such as soil depth.
4. Trait-matching between plants and herbivores was an important driver explaining the abundance and diversity of resource-acquisition traits within grasshopper communities. However, the presence of specific habitats in the surrounding landscape had also a strong influence on herbivore functional diversity in grasslands. Our study suggests that also mass effects are a central mechanism promoting higher functional diversity within animal communities in highly disturbed anthropogenic systems.

Key-words: land use intensification, body size, functional trait diversity, grasshoppers, grassland, incisor strength, metacommunity, plant-insect interactions, resource-acquisition traits

Introduction

Biotic interactions are a key driver of species coexistence (Tylianakis *et al*. 2008; Maire *et al*. 2012; Kraft, Godoy & Levine 2015), species diversity within and across communities (Kraft, Valencia & Ackerly 2008; Cornwell & Ackerly 2009; Gross *et al*. 2013) and ecosystem functioning (Belovsky & Slade 2000; Hooper *et al*. 2005; Duffy *et al.* 2007; Reiss *et al*. 2009; Deraison *et al*. 2015a). Understanding the importance of biotic interactions in shaping diverse plant and animal communities is inherently challenging (Gross *et al*. 2009; Reiss *et al*. 2009; Bartomeus *et al*. 2016; Gravel, Albouy & Thuiller 2016), due to the diversity of interactions (Tylianakis *et al*. 2008), and their spatial and temporal dynamics (Mouquet *et al.* 2003; Fukami *et al.* 2005). Identifying the ultimate determinants of biotic interactions within and across trophic levels is an emerging horizon in trait-based ecology with important implications for the development of a predictive framework linking biodiversity, trophic interactions and ecosystem functioning (Reiss *et al*. 2009; Lavorel *et al*. 2013; Deraison *et al*. 2015b; Bartomeus *et al*. 2016).

Functional traits are hypothesised to reflect the species niche (McGill *et al*. 2006; Devictor *et al*. 2010) and have been successfully used to predict the outcomes of biotic interactions within plant communities, as well as their importance at the community and ecosystem scales (e.g. Gross *et al.* 2009; see Funk *et al.* 2016 for a review). Recent studies suggested that trait-based approaches might equally apply to the study of trophic interactions between adjacent trophic levels (Reiss *et al*. 2009; van der Plas, Anderson & Olff 2012; Lavorel *et al*. 2013; Bartomeus *et al*. 2016; Gravel, Albouy & Thuiller 2016). The approach relies on the identification of traits that mediate the existing trophic linkages between adjacent trophic levels (i.e. "trait-matching", Garibaldi *et al*. 2015; Bartomeus *et al*. 2016). Trait-matching has been identified for many organisms (e.g. bird beak size and fruit size, Darwin 1872; plant corolla length and bee proboscis length, Fontaine *et al*. 2006; Garibaldi *et al*. 2015; energy diet and muscle mitochondrial density of marine predators, Spitz, Ridoux & Brind'Amour 2014). However, it is less known how trait-matching explains the abundance and the diversity of animal species across functionally diverse communities (Bartomeus *et al*. 2016).

Animal communities face recurrent disturbances, which may disrupt trophic interactions and decrease their importance in shaping the diversity and abundance patterns within a community (Grime 1973; Tylianakis *et al*. 2008; Valiente-Banuet *et al.* 2015). For instance, the relative importance of biotic interactions may increase with time after disturbance (Fukami *et al*. 2005). In addition, disturbance can operate at larger spatial scales (e.g. habitat fragmentation), affecting local community assembly by reducing the regional species pool and/or limiting dispersal between communities (e.g. Hillebrand & Blenckner 2002, Leibold *et al*. 2004; Valiente-Banuet *et al.* 2015). Integrating the metacommunity framework (Leibold *et al*. 2004), based on a system of local communities linked by dispersal, into trait-based approaches may help to reveal the relative contribution of trophic interactions and dispersal processes in determining community functional structure (Spasojevic *et al.* 2014).

In intensively managed agricultural systems, species are impacted by disturbance acting at local and landscape scales with important detrimental effects on species abundance, diversity and composition of ecological communities (Newbold *et al*. 2016). This is particularly true for taxa associated with perennial habitats such as grasslands (Clough *et al*. 2014; Kormann *et al*. 2015) because of: i) the direct destruction of their habitat leading to its increasing scarcity at the landscape level, e.g. due to their conversion to arable land (Kormann *et al*. 2015); ii) and the low quality of the remaining habitats due to the replacement of traditional extensively managed grasslands by low plant species richness, highly productive sown grasslands (Wesche *et al*., 2012). Understanding how grassland functional diversity within and across trophic levels responds to land use intensification at both local and landscape scales is a major concern for both biodiversity conservation and the management of important ecosystem services in farmlands (Larsen *et al.* 2005; Garibaldi *et al*. 2011; Newbold *et al.* 2015).

Grasshoppers represent the largest aboveground arthropod biomass in temperate grasslands (Báldi & Kisbenedek 1997). They have a considerable importance as primary consumers, nutrient recyclers and constitute the bulk of the diet of many birds in farmlands (Bretagnolle *et al*. 2011). The functional diversity of grasshopper communities is a key driver of their impact on plant communities (Deraison *et al*. 2015b) and is highly sensitive to the composition of local plant communities (van der Plas *et al*. 2012; Badenhausser *et al*. 2015). Strong matching between the strength of grasshopper mandibles (i.e. incisor strength) and plant leaf toughness has been recently demonstrated (Ibanez *et al*. 2013a). This resource-acquisition trait varies independently from body size and associated mobility traits across grasshopper species (Ibanez *et al*. 2013a; Deraison *et al*. 2015a). Consequently there is an exciting opportunity to disentangle the effects of trait-matching and dispersal processes on herbivore communities subject to increasing land use intensification at both local and landscape scales.

Here we used a trait-based approach with an extensive and detailed dataset on grasshopper and plant traits, from communities living in 204 sampled grasslands under intensive management regimes, to quantify how local, regional and temporal processes, modulated by land use intensification, impact local herbivore community structure. First, we evaluated the correlation between multiple grasshopper traits across the studied species pool, including grasshopper resource-acquisition traits, body size and mobility traits. Second, we tested the two following hypotheses: (i) the community level distribution of grasshopper resource-acquisition traits will be primarily determined by the functional composition of local (field scale) plant communities according to the trait-matching observed between grasshopper and plant species (Deraison *et al*. 2015a) (Fig. 1, hypothesis a); (ii) grasshopper body size and mobility-related traits will be more impacted by landscape parameters than resource-acquisition traits (Fig. 1, hypothesis b). Finally, we aimed to quantify the interactions between local and landscape factors related to land use intensification effects on herbivore communities (Fig. 1, hypothesis b and c). Land use intensification acting at the landscape scale may modulate its effect at the local scale by impacting the grasshopper species pool and the connectivity between grasslands, whereas the presence of source habitats may provide important mass effects (i.e. flows of individuals, Leibold *et al*. 2004; Spasojevic *et al*. 2014).

Materials and methods

STUDY AREA

The study was conducted in the Long Term Ecological Research area “Zone Atelier Plaine & Val de Sèvre” (ZAPVS) located in western France. The ZAPVS site covered 430 km^2 of an intensively managed agricultural plain, mostly dedicated to wheat crop production. In 2011, grasslands covered about 13% of the total surface, and were mainly composed of alfalfa or pure/mixed grass fields of varied age structure (temporary and permanent grasslands). Grasslands were not irrigated and none received any insecticide or herbicide treatment. Soils were mostly composed of karst, with calcareous rocks providing shallow calcareous soils with rather low water retention. Since 1994, land cover has been monitored yearly at the field scale

(14 000 fields approximately) by the CNRS research centre of Chizé (Bretagnolle *et al.* 2011). Around 30 categories of crop types were recorded as well as all roads/tracks, towns, forests, rivers and hedges. All information collected has been stored and managed in a Geographical Information System database, running on QGIS v 1.7.3 (QGIS Development Team 2012).

PLANT SURVEY AND PLANT FUNCTIONAL TRAITS

A botanical survey was conducted in July 2011 on 204 grasslands, selected randomly across the ZAPVS using our GIS database, in order to quantify grassland botanical diversity over the study area. In each grassland, we used 10 quadrats of 1m² located randomly within the grassland field to estimate plant diversity and plant species abundance. In each quadrat the number of species was recorded and a percent cover was visually estimated for each plant species. Relative abundance per species was then calculated as the sum of the species cover in the 10 quadrats divided by the total cover of all species. Selected grasslands represented a wide range of grassland types (13.2 % of pure sown alfalfa ≤ 5 years, 24.0 % of grasslands sown with pure grass seed or with seed sets including grass species and alfalfa or clover, 13.7 % of non-sown grasslands ≤ 5 years and 49.0 % of permanent grasslands > 5 years), ages (from 1 year to > 17 years) and uses (pasture, set-aside, meadow) in the ZAPVS which translated into a wide range of plant communities at the field scale (see Fig. S1, Appendix S1 in Supporting information).

We focussed on two plant functional traits: leaf dry matter content (LDMC) and leaf C:N ratio. LDMC reflects the biomechanical properties of the leaves (Deraison *et al*. 2015a). Leaf C:N ratio reflects the stoichiometry of the leaves. The traits are positively correlated with leaf toughness (Ibanez *et al*. 2013a) and negatively correlated with leaf thickness (see Fig. S1 in Appendix S1 for plant trait correlations). Together, these two plant traits are good predictors of grasshopper feeding niches (Deraison *et al*. 2015a). Plant trait data was extracted from a local trait database (Deraison *et al*. 2015a) (see Fig. S1, Appendix S1).

GRASSHOPPER SURVEY AND GRASSHOPPER FUNCTIONAL TRAITS

In late July 2011, grasshopper density was estimated as the number of individual grasshoppers per m² at the time of maximum adult density in the study area within the 204 surveyed grasslands (Badenhausser *et al.* 2009). Grasshoppers were sampled by removal trapping with a one square meter cage sampler (Badenhausser 2009) randomly thrown 10 times within the grassland field. The survey was conducted during the day from 10:00 to 16:00 and when temperatures were > 10°C (Badenhausser 2012). Rain that occurred during sampling survey was noted as it may influence grasshopper activity. All caught grasshoppers were collected by hand and individuals were sexed, identified to species level. All individuals were conserved in alcohol (70%) after identification. In total, we sampled 6484 grasshopper individuals among 17 species.

Grasshopper morphological traits were measured on the fifteen dominant species in the study area that represented more than 90 % of all individuals trapped since 2004 (Badenhausser 2012). We measured grasshopper incisor strength, a trait related to resource-acquisition which is an accurate predictor of grasshopper feeding niche (Ibanez *et al*. 2013a; Deraison *et al*. 2015a). We also measured traits related to mobility, i.e., body size, which is positively related to dispersal abilities (Reinhardt *et al*. 2005), wing shape and leg length (Harrison 1980).

Twenty individuals per species were measured and for each species we measured ten individuals per sex. Selected individuals were randomly chosen from the pool of individuals collected in 2011. All measurements were performed using a stereo microscope (Leica Microsystems M50) equipped with an integrated high definition microscope camera (Leica IC80

HD). Body size (mm) (BS) was measured as the length from the head to the femur apex of the posterior legs (Deraison *et al*. 2015a). We also measured wing length (WgL) and area (WgA), femur length (FmL), width (FmW) and surface (FmS), tibia length (TL) and calculated the ratio between wing area and body size. We measured the different components of incisor strength (IS) following Ibanez *et al*. (2013a):

$$\mathrm{IS} = \mathrm{A} * \frac{\mathrm{La}}{\mathrm{Li}} * \frac{1}{\mathrm{Ri}} \qquad \textit{(eqn 1)}$$

where Ri is the incisor region length, A the mandible section area, La the length of the adductor muscle lever and Li the length of the incisor lever.

STATISTICAL ANALYSES

All statistical analyses were performed using the R statistical software (R Development Core Team 2013) version 3.2.1.

Correlation between grasshopper traits

We performed a principal component analysis (PCA) on grasshopper species traits to evaluate how body size, mobility and resource-acquisition traits were correlated across the studied grasshopper species pool. We used a VARIMAX procedure to maximise the correlations between PCA axes and traits. This approach approximates the functional niche of grasshopper species (Devictor *et al*. 2010) defined as the relative position of each species in the functional trait space.

Characterisation of plant and grasshopper functional diversity in grassland

We characterised the functional structure of plant and grasshopper communities in each grassland by calculating the community-weighted mean and variance for each trait separately:

$$\text{Community mean}_j = \sum_i^n p_{ij} T_i \qquad \textit{(eqn 2)}$$

$$\text{Community variance}_j = \sum_i^n p_{ij} (T_i - \text{community mean}_j)^2 \qquad \textit{(eqn 3)}$$

where p_{ij} is the abundance of the species i in the community j and T_i the mean trait value of the species i. The mean trait value of the community is weighted by the species abundance and reflects the functional identity of dominant species in a given community. The variance of the community is a measure of the functional trait diversity within a given community. Calculated for each trait separately, it is similar to other weighted distance-based indices of functional diversity (e.g. Functional Dispersion, FDis, in Laliberté & Legendre 2010). For grasshoppers, the community mean value of incisor strength reflects the feeding niche optima while the community variance reflects the feeding niche breadth (Deraison *et al*. 2015b). Community means and variances were calculated following eqn 2 and 3 for incisor strength and for size and mobility traits. For plant species, the community mean and variance values were calculated for LDMC and C:N ratio following eqn 2 and 3. As the community variance values for LDMC and C:N ratio were highly correlated (r = 0.72, p-value< 0.001), we used the FDis index of Laliberté & Legendre (2010) as a combined measure of plant functional diversity considering the two traits together.

Effect of local and landscape factors on grasshopper functional diversity

We used multiple regression models to test for the effect of local and landscape factors on the means and variances of grasshopper community traits. We ran separate analyses on the community mean and variance values of the grasshopper selected traits to test our hypotheses (Fig.1). We included predictors of trait variation at two spatial scales:

(i) Local (field scale) metrics included the plant community attributes calculated for LDMC and plant C:N ratio (i.e. mean LDMC, mean C:N, FDis). Local land use intensification was characterised by the grassland age (Badenhausser & Cordeau 2012), calculated as the time elapsed since the last ploughing according to our land use GIS database. We also included soil depth categories (ranging from 1 to 4), extracted from the local GIS database, as a potential factor impacting grasshopper population dynamics (microhabitats, thermoregulation, oviposition sites, Uvarov 1977).

(ii) Landscape scale metrics were calculated in a 1 km-radius buffer centred on each grassland field. The scale of 1 km was chosen to approximate the maximal dispersal distance of the farmland grasshopper species (Reinhardt *et al*. 2005). Spatial data were extracted from the GIS database of the study area using QGIS v. 1.7.3. Landscape scale land use intensification was characterised by the percentage of annual crops within the buffer area (Fig. 1) (Kormann *et al*. 2015). In a first set of analyses (data not shown) we also included the percentage of temporary (i.e. grasslands with an age ≤ 5 years, sown with pure grass seed sets such as Ryegrass or with seed sets including grass species and alfalfa or clover, Fig. S1 in Appendix 1) and permanent grassland surfaces (defined as grassland with an age > 5 years) in the landscape. Since the percentage of crop cover was negatively correlated with the percentage of temporary and permanent grassland cover (r = -0.738), we included in the models either the percentage of crop cover or the percentage of grassland cover. As the best-selected models included the percentage of crop cover, we then only considered in the final models the effect of crop cover, i.e. the increasing scarcity of grassland cover at the landscape scale. We also considered a set of important landscape variables to account for any compositional effect of the landscape, including: (i) the percentage of pure alfalfa surfaces, all of which may provide mass effects as source habitats (Leibold *et al*. 2004; Spasojevic *et al*. 2014); (ii) the percentage of vineyard surfaces, which may act as favourable habitats for grasshoppers (Bruggisser, Schmidt-Entling & Bacher 2010); and (iii) the percentage of wood surfaces (i.e. small patches of remnant forests) which may act as barriers to dispersal (Mabelis *et al.* 1994; Gauffre *et al*. 2015).

Landscape metrics ranged from 40-95% for annual crops, 0-36% for temporary and permanent grasslands, 0-23% for alfalfa, 0-3% for vineyard and 0-45% for wood. We also calculated an index of landscape connectivity using the total length (m) of small roads and paths less than four meters wide. This metric is used as a proxy of uncultivated grassy habitats and connectivity between grasshopper source habitats (Badenhausser & Cordeau 2012). The selected landscape variables were not correlated (see Table S1 in appendix S2).

As disturbance due to intensive agricultural practices may alter trait-matching between plants and herbivores, we considered in the model two-way interactions between disturbance covariates at local (grassland age) or landscape (% annual crop) scales and the local scale predictors (soil depth and functional structure of plant communities). Quadratic terms for all predictors were included in order to account for potential non-linear effects.

To correct for additional spatial effects not accounted for by the local and landscape predictors, we included the coordinates of the centroid of each sampled grassland (latitude, X and longitude, Y). Further covariates accounted for sampling conditions were included: weather conditions (rain during the survey), recent mowing events (0/1 factor) and grazing (0/1 factor). The vast majority of grasslands were mown (82% of the sampled grasslands), while some were managed by grazing (18%). As increasing species richness and animal density may bias functional diversity metrics (Mayfield *et al*. 2010), we also included in the models grasshopper species diversity and density.

In a first step, we used a stepwise regression procedure, based on minimising the corrected Akaike information criterion (AICc), to select the most adequate set of polynomial terms. Then, a model selection procedure based on AICc selection (delta AICc < 2) was applied on the resulting full models to select the best predictors most supported by the data using the function *dredge* in the R package *MuMIn* (Barton 2014). Model averaging was performed based on AICc weight when multiple models were selected. Model residuals were inspected for constant variance and normality. All variables (predictors and response variables) were standardised (z-scored: mean-centred and divided by the standard deviation) to interpret parameter estimates on a comparable scale (Schielzeth 2010).

To evaluate the relative importance of the predictors under consideration as drivers of the grasshopper community structure, we calculated the relative effect of the parameter estimates for each set of predictors. This method is similar to a variance decomposition analysis since we z-scored all predictors prior to analysis.

Results

FUNCTIONAL AXES OF SPECIALISATION AMONG GRASSHOPPER SPECIES

The Principal Component Analysis (PCA) identified two main independent axes of functional specialisation that jointly accounted for 84% of the total variance among grasshopper species traits (Fig. 2, see also Table S2 in Appendix S3). The first PCA axis (67% of variance explained) was positively correlated with mobility-related traits - body size (BS), wing size (Wg), tibia length (Tbl), femur length (Fml), femur width (Fmw) and femur surface (Fms). The second PCA axis (17% of variance explained) was positively correlated with resource-acquisition traits - incisor strength (IS) and the ratio between the length of the adductor muscle lever and the length of the incisor lever (La/Li). In agreement with previous studies (Ibanez *et al*. 2013a; Deraison *et al*. 2015a), we confirmed that resource-acquisition traits varied independently from mobility-related traits (body size and other mobility traits) across the studied grasshopper species pool. Consequently, for the subsequent analyses, we selected the two traits, incisor strength and body size, as functional markers of the two functional axes of specialisation, to investigate herbivore community responses to land use intensification.

EFFECT OF LOCAL AND LANDSCAPE FACTORS ON GRASSHOPPER RESOURCE-ACQUISITION TRAIT

Both local and landscape factors were related to variation in community mean incisor strength and variance of incisor strength (Fig. 3; see also Tables S3 and S4 for more details about model selection and model parameters in Appendix S4), with an $R^2 = 0.29$ and 0.51, respectively, for the top models (AICc-based model selection, see Appendix S4). Interestingly, over 50% of the variance explained for mean incisor strength was due to local variables, while for the community variance of incisor strength it was largely due to landscape variables (around 60% of the explained variance Fig. 3).

Specifically, plant community traits and grassland age accounted for 50% of the explained variance of mean incisor strength (Fig. 3a), mostly due to a positive effect of plant community mean leaf dry matter content (LDMC) (30% of explained variance, p-value<0.001). This suggests that plant communities with tough leaves (high LDMC) favour grasshopper species with strong incisors. In addition, grassland age had a negative effect on the mean incisor strength (explained variance 12%, p-value=0.016), suggesting that in older grasslands the abundance of grasshoppers with weaker incisors increased. Landscape variables accounted for 40% of the explained variance.

The variance of incisor strength of grasshopper communities was related to local variables accounting for 24% of the explained variance, without interactions (Fig. 3b). Local effects were determined by a positive effect of plant functional diversity (FDis, explained variance 18%, p-value<0.001), indicating that functionally diverse plant communities host more diverse herbivore communities. This effect is modulated by the grassland age (explained variance 10%), where old and functionally diverse plant community maximised the variance of incisor strength (Fig. 4). Landscape variables accounted for 59% of the explained variance, given by a positive effect of wood (p-value<0.001, see also Fig. S2 in Appendix S5) and alfalfa (p-value=0.034) cover in the surrounding landscape.

EFFECT OF LOCAL AND LANDSCAPE FACTORS ON GRASSHOPPER BODY SIZE

Both local and landscape factors and their interactions were related to variation in grasshopper body size (Fig. 5, see also Tables S3 and S4 for more details about model selection and model parameters in Appendix S4), with an $R^2 = 0.29$ and 0.40, respectively, for the top models (AICc-based model selection, see Appendix S4). For the mean body size of grasshopper communities, local variables accounted for around 30% of the explained variance, while landscape variables explained around 30% of the explained variance, with the remaining 40% due to interactions between local and landscape variables (Fig. 5a).

The mean body size increased with a higher percentage of vineyards in the surrounding landscape (p-value=0.002, explained variance 15%) and in grasslands with deeper soils (p-value=0.001, explained variance 16%). In addition, the effect of the percentage of annual crops in the landscape was modulated by soil depth (p-value = 0.05) and plant FDis (p-value = 0.006) (see interactions in Fig. S3, Appendix S5). Body size increased with the landscape-level proportion of crop cover in shallow soil and in grasslands characterised by low FDis (Fig. S5a). There was a significant interaction between grassland age and soil depth (p-value=0.006, Fig. 5). When increasing grassland age, body size decreased in deep soils while it tended to increase in shallow soils (Fig. S3 in Appendix S5).

For the variance of body size in grasshopper communities, local variables accounted for 60% of the explained variance and landscape variables for the remaining 40% (Fig. 5b). Soil depth had a negative effect on the variance of grasshopper body size (p-value=0.001, explained variance 23%), which suggests that grasshopper communities are less functionally diverse in grasslands established on deep soil. Plant mean C:N ratio had a positive effect on the variance of body size (p-value=0.005, explained variance 20%), suggesting that grasshopper communities are more functionally diverse in grasslands with a high C:N ratio. The percentage cover of vineyard in the surrounding landscape had a positive effect on the variance of body size (p-value=0.006, explained variance 17%), as did the percentage cover of alfalfa, albeit with a quadratic effect (p-value=0.010, explained variance 17%), leading to a decreasing variance in landscapes with higher alfalfa cover (see Fig. S4 in Appendix S5).

Discussion

We used a multi-trait approach to quantify the relative contribution of trait-matching and land use intensification to animal functional diversity. We showed that trait-matching between plants and herbivores is an important driver explaining the abundance and diversity of resource-acquisition traits within herbivore communities. However, herbivore functional diversity in grasslands cannot be understood without taking into account the presence of specific habitats in the surrounding landscape (Figs. 3 and 5). This suggests that mass effects (sensu Leibold *et al*. 2004) are a central factor determining trait diversity in herbivore communities.

TRAIT-MATCHING AND HERBIVORE DIVERSITY OF RESOURCE-ACQUISITION TRAITS

Trait-matching between plant and herbivore species explained herbivore trait abundance and diversity within communities. Consistent with predictions (Ibanez *et al*. 2013a; Deraison *et al*. 2015a), increasing leaf toughness within plant communities led to an increase in the abundance of grasshopper species with strong incisors while plant communities with softer leaves promoted the abundance of grasshopper species with weaker incisors (Fig. 3a). Similarly, increasing plant functional diversity increased the functional diversity of resource-acquisition traits in herbivore communities (Fig. 3b). These two results suggest that incisor strength is a key trait explaining feeding niche partitioning within and between herbivore communities.

Leaf toughness, positively correlated with LDMC (Ibanez *et al*. 2013a), has been hypothesised to act as a physical barrier trait against herbivory, whereby grasshoppers characterised by weak incisor strength are not able to eat tough leaves (Clissold 2007). Following this hypothesis, plant communities with soft leaves (low LDMC) would be expected to support more diverse herbivore communities than plant communities with tough leaves (high LDMC), suggesting a negative correlation between plant community leaf toughness and herbivore functional diversity (Ibanez *et al*. 2013b). Yet, we did not observe such relationships but rather a positive effect of plant trait diversity on herbivore functional diversity (Fig. 3b). This result is consistent with the feeding niche complementarity hypothesis (Ibanez *et al*. 2013a; Deraison *et al*. 2015a), whereby increasing the availability of different feeding niches facilitates the coexistence of grasshopper species characterised by contrasting incisor strengths and feeding preferences. To the best of our knowledge, our study is therefore one of the few able to explicitly link trait-matching to abundance.

RESOURCE-ACQUISITION TRAITS, LOCAL DISTURBANCE AND LANDSCAPE CONTEXT

Grassland age modulated the effect of trait-matching on the functional structure of herbivore communities (Fig. 4). The positive effect of plant diversity on the diversity of resource-acquisition traits is maximised in older grasslands (Fig. 4) suggesting that the importance of trophic interactions in structuring herbivore communities may increase with time. This result echoes previous studies on the role of assembly time in shaping patterns of plant diversity (e.g. Chase 2003; Fukami 2004). Trophic interactions in grasshopper communities were considerably more affected by field-scale disturbance (i.e., time since the last ploughing) than by landscape disturbance. This may indicate that assembly time is more important than dispersal limitation due to increased annual crop cover in the landscape even in highly simplified agricultural landscapes, at least at the spatial scales considered in our study area.

In addition to trait-matching, the functional diversity of herbivore traits within communities was explained to a large extent by landscape-scale mass effects (Leibold *et al*. 2004), i.e., the presence of specific habitats in the surrounding landscape sustaining a flow of functionally contrasted species across communities. This suggests that mass effects are central factors determining functional diversity within herbivore communities. It also suggests that the functional-trait approach needs to incorporate more than local niche-based processes and would benefit from considering metacommunity processes, such as dispersal and mass effects, to fully understand community assembly in fragmented landscape (see also Martins *et al*. 2014, Gámez-Virués *et al*. 2015).

Specifically, the percentage of wood and alfalfa cover in the landscape surrounding focal grasslands had strong impacts on the functional diversity of resource-acquisition traits (up to 60% of the explained variance, Fig. 3b). Although few grasshopper species are forest species in temperate systems (Uvarov 1977), the presence of woods in the landscape surrounding the focal grasslands is favourable for specific species (e.g. *Gomphocerippus rufus*, *Pezotettix giornae* in wood edges, Bellmann & Luquet 1995) with extreme incisor strength values (Fig. 2). Similarly, artificial grasslands dominated by alfalfa, a plant characterised by soft leaves (Deraison *et al*. 2015a), can support large populations of *Calliptamus italicus* (Badenhausser 2012), a grasshopper species with weak incisors (Deraison *et al*. 2015a). Thus grasshopper species with contrasted trait values, associated with woods and alfalfa fields present in the surrounding landscape, may disperse and enhance functional trait diversity in focal grasslands.

HERBIVORE BODY SIZE AND LANDSCAPE SIMPLIFICATION

We partially validated our hypothesis that simplified landscapes dominated by annual crops select for larger (more mobile) herbivore species (Fig. 1, hypothesis b, Fig.5, Fig S3). However, the body size response to increasing annual crop cover was modulated by local factors (significant interactive effect between local and landscape predictors, see Fig. 5). Contrary to incisor strength for which a direct linkage with grasshopper feeding niche has been identified, body size is an integrative trait related to multiple facets of animal species physiology and ecology (e.g. metabolism, Brown *et al.* 2004; thermoregulation, Uvarov 1977; mobility and dispersal, De Bie *et al*. 2012, Chappell & Whitman 1990; and stoichiometry Hillebrand *et al*.

2009; Deraison *et al*. 2015a). This may explain the interactive effect observed between local and landscape factors on body size distribution within grasshopper communities. While further investigations are needed to fully understand the interactive effect of local and landscape factors, our results suggested two independent ways by which local and landscape factors shape herbivore body size:

(i) The significant interactions between annual crop cover or grassland age and soil depth (Fig. S3) may suggest that mobility and microclimatic niches of grasshopper species modulated body size responses to land use intensification (Kéfi *et al*. 2012; De Bie *et al*. 2012). Simplified landscapes with a high cover of annual crops and recently sown grasslands were generally dominated by large and mobile grasshoppers (such as the open-landscape species *C. italicus*). However, this was particularly true where soil depth was low because shallow soils are likely to benefit large grasshoppers by allowing them to warm up more easily (Uvarov 1977; Chappell & Whitman 1990). This observation might be further supported by the positive effect of vineyards on grasshopper body size (Fig. 5). Remnant vineyards are known to provide specific habitats to warm up for large grasshoppers characterised by high movement abilities, such as Oedipodae species originated from Mediterranean areas (e.g. *Oedipoda caerulescens*, *Aiolopus thalassinus*, see Uvarov 1977). In complex landscapes, large grasshoppers were more common on deep soils. A possible explanation could be that such soils are associated to wetlands, dominated by large grasshoppers with low thermal demands, such as *Mecosthetus parapleurus* and *Stethophyma grossum* (Uvarov 1977; Chappell & Whitman 1990).

(ii) We also found a significant effect of plant mean C:N ratio on the variance of grasshopper body size (Fig. 5). Body size is not directly related to feeding preferences of grasshoppers (Ibanez *et al.* 2013a; Deraison *et al.* 2015a). However, large grasshopper species (e.g *C. italicus*) are characterised by lower C:N ratio and higher N demand than smaller species (Hillebrand *et al*. 2009; Deraison *et al*. 2015a). At the community level, the relationship between grasshopper body size and their C:N stoichiometry may explain the response of body size variance to plant C:N ratio. A local effect of plant C:N ratio is also consistent with the detection of a significant effect of alfalfa cover at the landscape scale on body size variance (Fig. 5), a perennial crop characterised by low C:N ratio (Fig. S1). Grasshopper stoichiometry may represent an additional dimension, yet unexplored, by which herbivore communities respond to land use intensification acting at both local and landscape scales. Investigating the interplay between microclimatic niches, herbivore stoichiometry and mobility may offer promising perspectives to understand how body size of ectothermic species varies within and across communities.

IMPLICATIONS FOR TRAIT-BASED APPROACH AND CONSEQUENCES OF LAND USE INTENSIFICATION

Resource partitioning between co-occurring species is a central hypothesis to explain observed species coexistence (Chesson 2000) and associated high functional diversity within plant (Cornwell & Ackerly 2009; Gross *et al*. 2013) and animal communities (Kartzinel *et al.* 2015; Deraison *et al*. 2015b). Recent studies on plant trait diversity in more pristine terrestrial systems (e.g. Spasojevic *et al*. 2014) have generally found smaller impacts of landscape factors on local diversity than the one reported in our study. Similarly, studies focusing on arthropod species diversity in grasslands (e.g. Schaffers *et al*. 2008) have found higher impacts of local factors than landscape factors. Our study conducted in a highly disturbed anthropogenic system and focusing on plant-herbivore trait-matching suggests that in addition to local niche-based processes, mass effect and assembly time are central mechanisms promoting higher functional diversity of resource-acquisition traits within animal communities. It further adds to the growing evidence from comparative (Stevens *et al*. 2014) and experimental (Venail *et al*. 2008) studies indicating that dispersal and habitat specialisation jointly determine the trait distribution of animal communities in fragmented landscapes. Our study shows that the development of the trait-based approach would benefit from metacommunity theory in order to elucidate how multiple assembly processes operating at multiple spatial and temporal scales impact on resource-acquisition traits and mobility-related traits separately.

Our study may help to understand the consequences of land use intensification across spatial scales. Trait-matching and resource partitioning between functionally contrasted herbivore species clearly indicated that functionally diverse grasslands are highly beneficial to sustain functionally diverse herbivore communities. The importance of assembly time (Mouquet *et al*. 2003) suggests that converting functionally rich permanent grasslands toward sown grasslands (Wesche *et al*. 2012) may be particularly deleterious for herbivore functional diversity in agricultural landscapes. However, the negative impact of local land use intensification on the diversity of resource-acquisition traits can be mitigated by the presence of source habitats in the surrounding landscape, which may provide mass effects (e.g. woods, vineyards). Grassland isolation and landscape configuration appear far less important in our models than the composition of the landscape (see Kärnä *et al*. 2015 for a similar finding for aquatic insect communities) suggesting that conserving functionally diverse arthropod communities locally requires a diverse composition of agricultural landscapes.

Overall, our finding based on trait-matching and feeding niche differences between herbivore species could be easily extended to other important taxa in agricultural landscapes for which trait-mediated interactions have been identified (e.g. pollinators and predators, Gagic *et al.*

2015; Bartomeus *et al*. 2016). This may help to develop a predictive framework to manage and mitigate the effects of land use intensification on trophic interactions, biodiversity and associated ecosystem services.

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Data Accessibility

Data deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.ns143, (Le Provost *et al*. 2016).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. *Plant functional traits*

Fig. S1. Co-variations between plant community-weighted mean traits across grasslands in a principal component analysis (PCA).

Appendix S2. *Explanatory variables*

Table S1. Correlations among all predictors included in the models (r).

Appendix S3. *Grasshopper trait correlations*

Table S2. Correlations between traits and PCA axes (r).

Appendix S4. *Model selections*

Table S3. Model selection table.

Table S4. Best models selected from the multiple regressions.

Appendix S5. *Quadratic or interactive effects*

Fig. S2. Predicted effects of % crop, soil depth (categories), plant FDis and grassland age on community mean body size.

Fig. S3. Predicted effect of soil depth, age and % of crop cover on community mean body size.

Fig. S4. Predicted effect of % of alfalfa cover on community variance body size.

FIGURE LEGENDS

Figure 1 Hypothetical relationships between the functional structure of grasshopper communities and local or landscape factors in intensively managed agricultural landscapes.

Hypothesis (a): Herbivore resource-acquisition traits (i.e. mandible traits, incisor strength) are impacted by the functional structure of plant communities. According to plant herbivore trait-matching (Ibanez *et al*. 2013a; Deraison *et al*. 2015a), plant communities characterised by high leaf dry matter content (LDMC) and C:N ratio will select grasshoppers with strong mandibles. Plant communities characterised by low LDMC will select grasshopper species with weaker mandibles. Functionally diverse plant communities support more diverse herbivore communities (Deraison *et al*. 2015b).

Hypothesis (b): Herbivore mobility-related traits (body size, wing length) are impacted by the landscape context. Crop dominated landscapes will select for more mobile grasshopper species (Ronce 2007). The presence of favourable source habitats (e.g. % grassland) may increase grasshopper functional diversity (mass effects, Leibold *et al*. 2004; Spasojevic *et al*. 2014).

Hypothesis (c): The age of the grassland (time since last ploughing) determines the importance of trophic interactions in shaping the diversity and abundance patterns within herbivore communities (Mouquet *et al*. 2003). Trait-matching will explain grasshopper abundance in old grasslands. In young grasslands, no relationship is expected between plant and herbivore traits due to recent disturbance history (i.e. ploughing) (Fukami *et al*. 2005). Grasshopper functional diversity increases with grassland age (Deraison *et al*. 2015b).

Figure 2 Co-variation between male and female grasshopper species traits in a principal component analysis (PCA). The two orthogonal axes explain respectively 67% and 17% of the total variance. Traits are in italic black, species are in grey. Traits abbreviations: A, mandible section area (mm^2); IS, incisor strength; La/Li, ratio between La the length of the adductor muscle lever and Li the length of the incisor lever; Ri, incisor region length ; BS, body size (mm); Fml, femur length (mm); Fmw, femur width (mm); Fms, femur surface (mm^2); Tbl, tibia length (mm); Wg, wing size (mm^2); Wg:BS, ratio between wing and body size (mm^2 :mm). Grasshopper species abbreviations are As: *Aiolopus strepens,* At : *Aiolopus thalassinus,* Ca : *Chorthippus albomarginatus,* Cb : *Chorthippus biguttulus,* Cd : *Chorthippus dorsatus,* Ci : *Calliptamus italicus,* Ed : *Euchortippus declivus,* Ee : *Euchortippus elegantulus,* Gr : *Gomphocerippus rufus,* Ma : *Mecosthethus aliaceus,* Oc : *Oedipoda caerulescens, Oh : Omocestus haemorhoidalis,* Or : *Omocestus rufipes* , Pp : *Pseudochorthippus parallelus,* Pg : *Pezotettix giornae* and Ss : *Stenobothrus stigmaticus.* We added M for male and F for female.

Figure 3 Parameter estimates (± 95% confidence interval) resulting from the model averaging procedure and relative effects of estimates (%) of each group of predictors (i.e. local abiotic variables, local plant community, landscape variables) and their interactions on community mean incisor strength (a) and community variance incisor strength (b). P-values of the best selected models for each model parameter are given, *, *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001. Grasshopper community variance incisor strength was log-transformed and all explanatory variables were scaled (see also Tables S3 and S4 for more details in model selections and model parameters in Appendix S4).

Figure 4 Predicted community variance incisor strength (response surface) as a function of plant functional diversity (FDis) and the age of the grassland since the last ploughing event. The response variable is scaled to facilitate comparisons (see also Table S4, Appendix S4 for model parameters). Black dots indicated predicted values for each sampled grassland.

Figure 5 Parameter estimates (±95% confidence interval) resulting from the model averaging procedure and relative effects of estimates (%) of each group of predictors (i.e. local abiotic variables, local plant community, landscape variables) and their interactions on community mean body size (a) and community variance body size (b). P-values of the best selected models for each model parameter are given, *, *p-value* < 0.05; ** *p-value* < 0.01; *** *p-value* < 0.001. Grasshopper community variance body size was log-transformed and all explanatory variables were scaled (see also Tables S3 and S4 for more details in model selections and model parameters in Appendix S4).

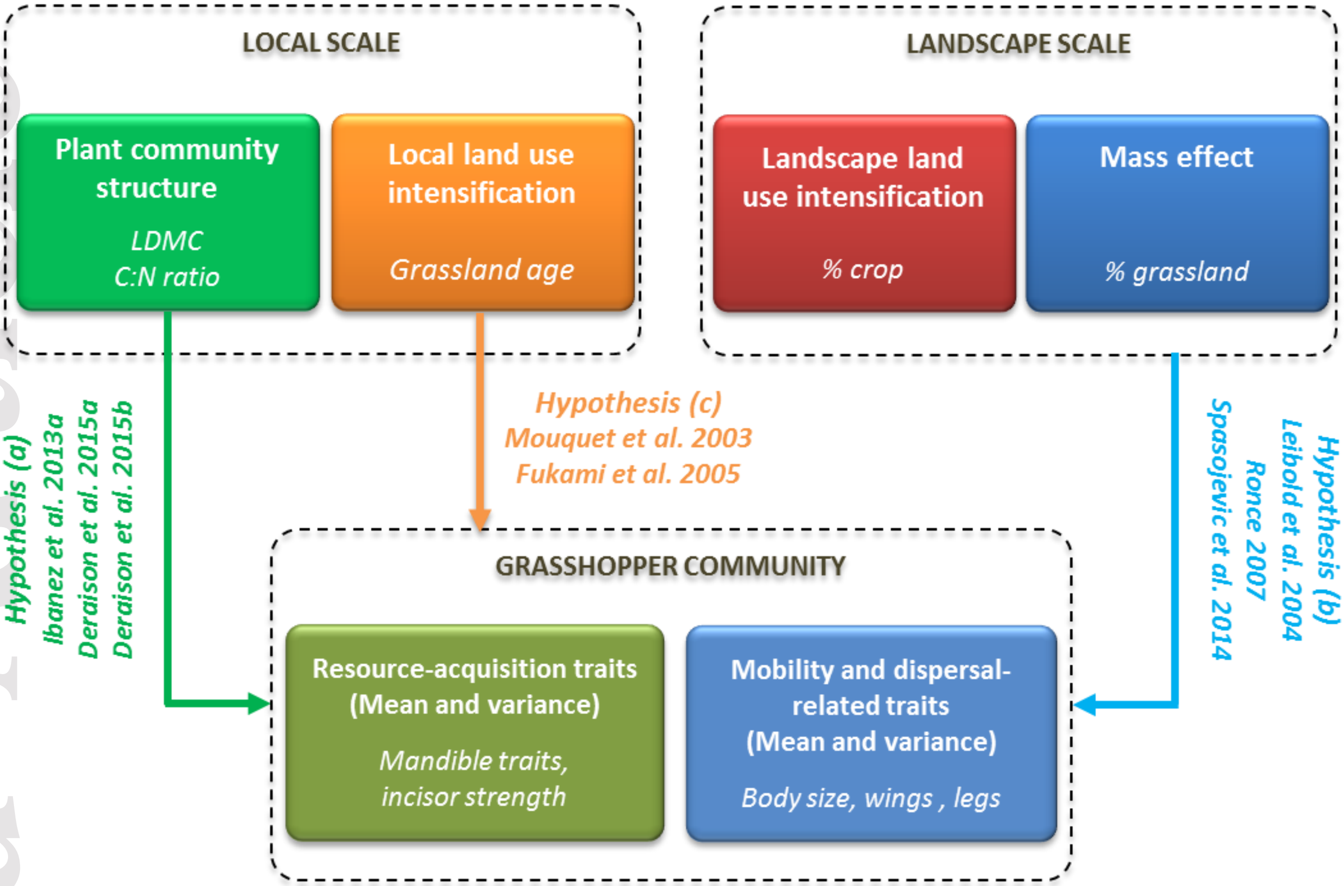

LOCAL SCALE
Plant community structure
LDMC
C:N ratio
Local land use intensification
Grassland age
LANDSCAPE SCALE
Landscape land use intensification
% crop
Mass effect
% grassland
Hypothesis (a)
Ibanez et al. 2013a
Deraison et al. 2015a
Deraison et al. 2015b
Hypothesis (c)
Mouquet et al. 2003
Fukami et al. 2005
Hypothesis (b)
Leibold et al. 2004
Ronce 2007
Spasojevic et al. 2014
GRASSHOPPER COMMUNITY
Resource-acquisition traits (Mean and variance)
Mandible traits, incisor strength
Mobility and dispersal-related traits (Mean and variance)
Body size, wings , legs

Fig. 1.

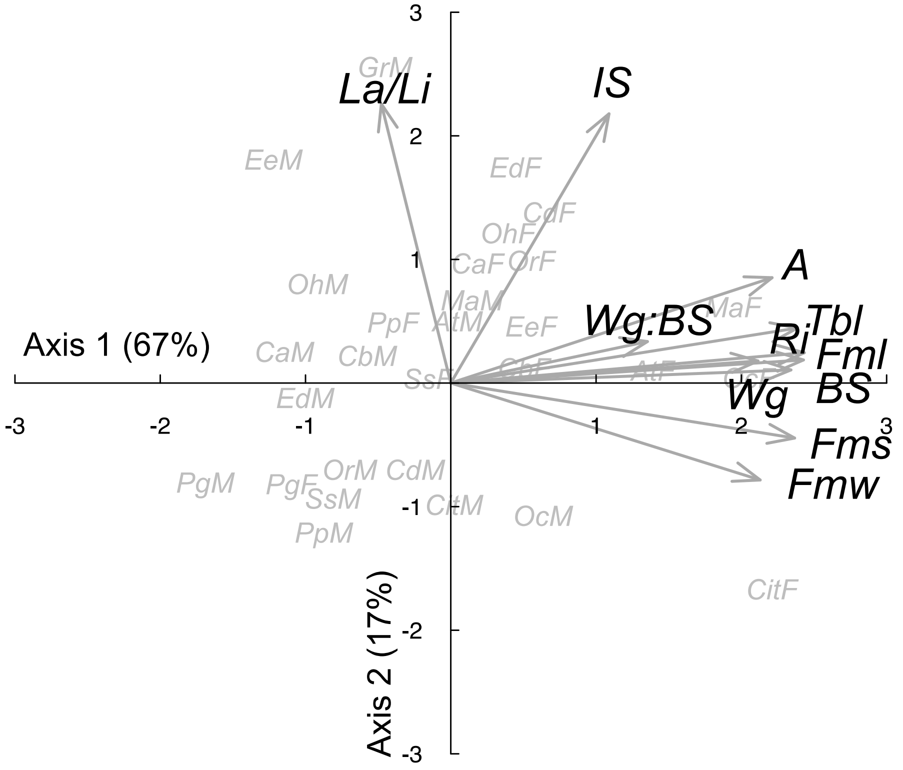
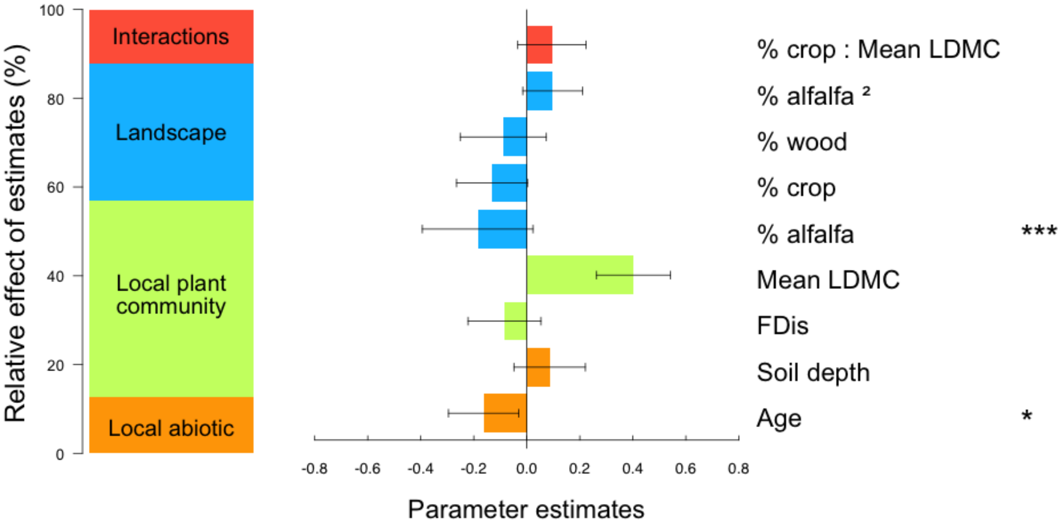

GrM
La/Li
IS
EeM
EdF
CdF
OhF
CaF
OrF
OhM
A
MaM
MaF
PpF
AtM
EeF
Wg:BS
Tbl
Ri
Fml
Axis 1 (67%)
CaM
CbM
ChF
AtF
SsF
OcF
Wg
BS
EdM
Fms
PgM
PgF
OrM
CdM
SsM
Fmw
CitM
OcM
PpM
CitF
Axis 2 (17%)
3
2
1
-1
-2
-3
-3
-2
-1
1
2
3

Fig. 2.

(a) **Mean incisor strength**



(b) **Variance incisor strength**

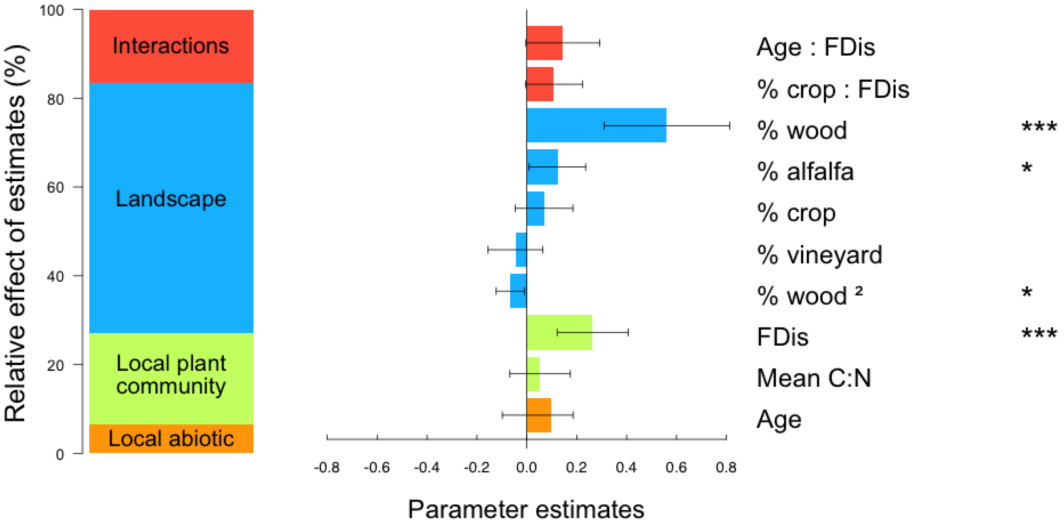


Fig. 3.

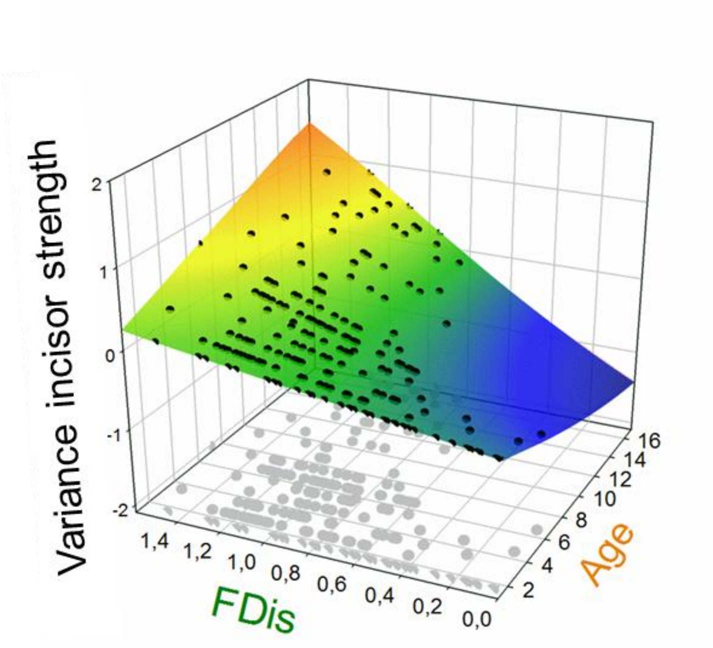
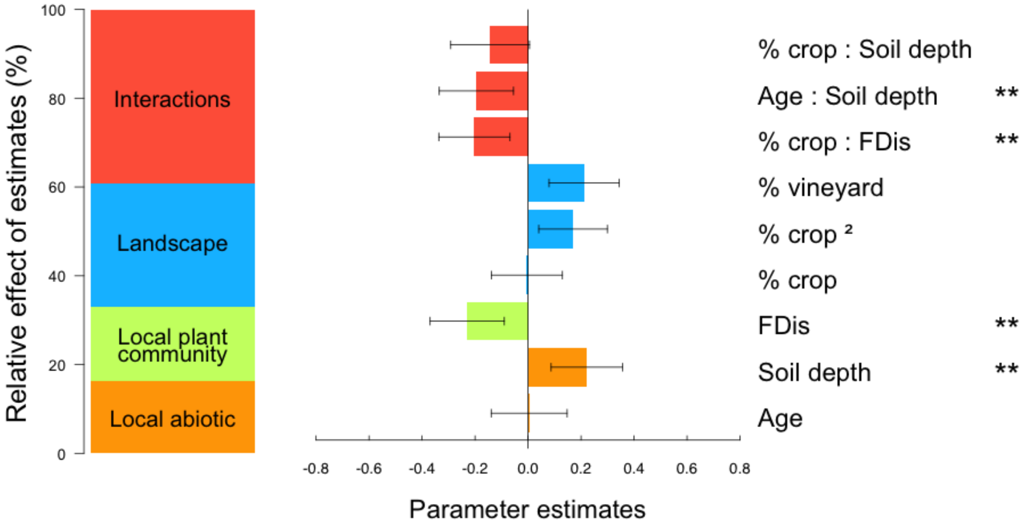

Variance incisor strength
2
1
0
-1
-2
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0,0
FDis
2
4
6
8
10
12
14
16
Age

Fig. 4.

(a) Mean body size



(b) Variance body size

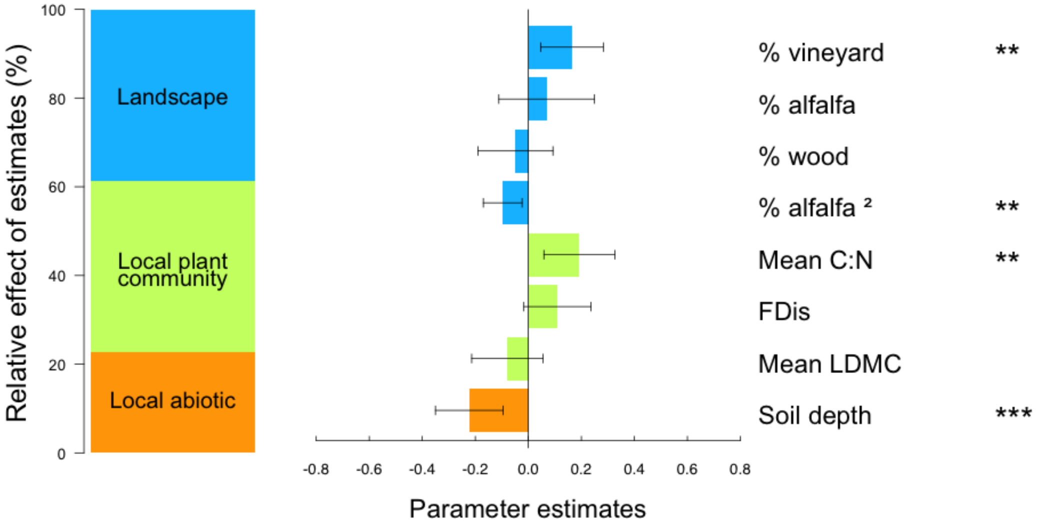


Fig. 5.