

## Natural habitat loss and exotic plants reduce the functional diversity of flower visitors in a heterogeneous subtropical landscape

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### Summary

**1.** Functional diversity (FD) of pollinators can increase plant reproductive output and the stability of plant-pollinator communities. Yet, in times of world-wide pollinator declines, effects of global change on pollinator FD remain poorly understood. Loss of natural habitat and exotic plant invasions are two major drivers of global change that particularly threaten pollinator diversity.

**2.** In a subtropical South African landscape, we investigated changes in the FD of flower visitor assemblages on native and exotic plants along gradients of natural habitat loss and relative abundance of exotic plants. We used a data set of 1434 flower visitor individuals sampled on 131 focal plants and calculated the FD in three flower visitor traits that are strongly related to plant–flower visitor interactions and pollination processes: proboscis length, proboscis diameter and body length.

**3.** Multivariate FD of flower visitors decreased with both increasing natural habitat loss and relative exotic abundance. Importantly, changes in FD went beyond those in flower visitor richness. Furthermore, flower visitor richness was not related to either natural habitat loss or relative exotic abundance. Loss in multivariate FD seemed to be mediated by complementary reductions of FD in proboscis length with natural habitat loss and of FD in body length with both global change drivers. Correspondingly, we recorded lower abundances of long-tongued flower visitors with natural habitat loss and reduced variance in body size with both drivers. In contrast, FD in proboscis diameter was unaffected by either driver. All effects of the two global change drivers were non-interactive.

**4.** Our results show that both natural habitat loss and exotic plants negatively affect flower visitor FD, which may imperil pollination of specialized plant species in degraded habitats. In contrast, flower visitor richness may not cover all facets of flower visitor FD that are relevant to pollination processes. Distinct responses of visitor traits to the two drivers suggest limited options to infer relations of one trait to another. Finally, additive effects of natural habitat loss and exotic plant invasions highlight the need to consider multiple drivers of global change when investigating ecosystem processes at a community scale.

**Key-words:** agricultural intensification, ecosystem functioning, ecosystem process, global change, plant invasion, plant reproduction, plant-pollinator interactions, specialization

### Introduction

Functional diversity (FD) – the diversity of species' properties that influence their individual performances (McGill *et al.* 2006; Schleuter *et al.* 2010) – is an integral part of biodiversity. Species communities with high FD are often more productive and stable (Díaz & Cabido 2001; Loreau & de Mazancourt 2013). For pollinator communities, FD

can be the result of interspecific variation in behavioural or morphological traits such as differences in flower handling or the size of mouthparts (Fontaine *et al.* 2006; Albrecht *et al.* 2012). Interspecific variation often results in niche partitioning and functional complementarity of pollinators, which can increase plant reproductive output and crop yield (Hoehn *et al.* 2008; Blüthgen & Klein 2011; Albrecht *et al.* 2012). Variation in functional traits of pollinators thus may be the primary driver behind the often-observed positive relationship between pollinator

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richness and pollination processes (e.g. Garibaldi *et al.* 2013). Studying the FD of pollinator communities along environmental gradients thus is a promising approach to predict consequences of changing environments for the structure and persistence of plant-pollinator communities (McGill *et al.* 2006; Potts *et al.* 2010; Williams *et al.* 2010). A deeper understanding of these processes is particularly important in times of world-wide pollinator declines, which are widely believed to result from human-induced global change (Vitousek *et al.* 1997; Potts *et al.* 2010).

Plant species within subtropical and tropical forests are especially dependent on animal pollinators for reproduction (Bawa *et al.* 1985; Ollerton, Winfree & Tarrant 2011). However, these forests are increasingly under pressure from the loss of natural habitat and invasions by exotic plants (Chapin *et al.* 2000; Sala *et al.* 2000). Numerous studies have investigated the effects of these two drivers of global change on plant-pollinator interactions, and effects seem to a large extent to be negative (Montero-Castaño & Vilà 2012 and references therein). Yet, most studies generally focus on pollinator richness and abundance as proxies for changes in the composition of pollinator communities.

In contrast, effects of natural habitat loss and exotic plant invasions on the FD of pollinator communities are poorly understood, although several studies suggest that losses are likely. Overall, simplified agricultural landscapes seem to support less functionally diverse insect communities than do structurally complex natural habitats (e.g. Tscharncke *et al.* 2008). For pollinators, a loss in FD could result from negative effects of habitat loss on small and immobile species (Greenleaf *et al.* 2007; Brückmann, Krauss & Steffan-Dewenter 2010). Similarly, the dominance of a single or few exotic plant species could trigger a loss in pollinator FD as the amount and diversity of native floral resources decrease (Traveset & Richardson 2006). Importantly, changes in pollinator FD associated with habitat loss or plant invasion are likely to differ among different investigated functional traits of pollinator species, and opposing responses of different functional traits may be masked when solely focussing on multivariate FD (Spasojevic & Suding 2012). Thus, both multivariate and univariate measures of FD are needed to disentangle changes in pollinator FD and their underlying mechanisms. Moreover, interactive, that is antagonistic or synergistic, effects between habitat loss and plant invasion are generally believed to strongly increase the risk of pollinator and associated native plant species decline (Biesmeijer *et al.* 2006; Didham *et al.* 2007; Potts *et al.* 2010). While not yet empirically studied, synergistic effects of the two drivers thus are a likely threat to the FD of pollinator communities in highly disturbed habitats.

Here, we studied the combined effects of natural habitat loss and exotic plants on the FD of communities of insect flower visitors in a subtropical South African landscape. As a measure of FD, we investigated multivariate and univariate functional dispersion (FDis; Laliberté & Legendre 2010) in three visitor traits that are strongly related to

plant-flower visitor interactions and pollination processes: proboscis length, proboscis diameter and body length (Greenleaf *et al.* 2007; Stang *et al.* 2009; Ibanez 2012). We hypothesized a decrease in multivariate FD of flower visitors with both global change drivers. We expected this decrease to be caused by reductions in univariate FD among the three flower visitor traits, with separate responses of individual visitor traits to the two drivers. Finally, we expected negative synergistic effects between the two drivers on pollinator FD.

## Materials and methods

### STUDY AREA

We conducted our study in a heterogeneous subtropical landscape within and around Oribi Gorge Nature Reserve (30°S, 30°E; 1850 ha), near the south coast of KwaZulu-Natal, South Africa. The natural vegetation in the region is characterized by indigenous scarp forests, which are interspersed by patches of natural grassland (Cooper 1985; Eeley, Lawes & Reyers 2001). However, most grassland has been converted into sugar cane fields, and the remaining scarp forests have been drastically reduced in their distribution and extent by the intensification of land use and urban sprawl (von Maltitz 2003). Furthermore, numerous exotic plant species are serious pests in the region and scarp forest edges are often heavily invaded by exotic plants such as *Lantana camara* (Verbenaceae), *Acacia mearnsii* (Fabaceae) and *Ageratum conyzoides* (Asteraceae). However, not all scarp forests are invaded to the same degree, regardless of whether they are situated within nature reserves or the agricultural matrix. Consequently, the remaining natural habitat cover and the abundance of exotic plants along scarp forest edges are not generally correlated. Accordingly, we were able to separate the effects of loss of natural habitat and relative exotic plant abundance on flower visitor FD in this subtropical landscape.

### STUDY DESIGN

In September 2011, we established 17 study sites, located in forests within and around Oribi Gorge Nature Reserve. Mean pair-wise distance between study sites ranged from 697 to 21,292 m (mean  $\pm$  SD: 8521  $\pm$  153 m). In each site, we established one permanent 100-m-long and 4-m-wide transect situated at forest edges. As stated above, forest edges were chosen as they represented centres of exotic plant abundance, but also to assure comparability of intensities of edge effects on communities of flower visitors across study sites. Establishing study sites within forests would have confounded results owing to stronger edge effects in forest remnants than in continuous forest (Saunders, Hobbs & Margules 1991).

To quantify natural habitat loss, we estimated the percentage of remaining natural habitat (scarp forests, small patches of remaining grassland) in a 500 m radius surrounding the centre of each transect in a given study site, using digital maps and a regional land cover data set (Ezemvelo KZN Wildlife 2011). We expected this radius to be covered by the majority of flying insect flower visitors (Greenleaf *et al.* 2007), yet natural habitat cover in the 500 m radius was also strongly correlated to the cover in smaller and larger radii (250–2000 m). Loss of natural habitat was then defined as the proportion of the remaining non-natural habitat cover in the 500 m radius. To quantify the proportion of exotic plants on the total plant community in each study site, we performed transect walks every 10–14 days during the field season and estimated the floral abundance of flowering angiosperm species [in floral units; (Dicks, Corbet & Pywell 2002)]. We then

classified species into natives and exotics and calculated the mean relative exotic abundance on the total flower display per transect over all transect walks (varying between 0 and 1; i.e. no exotic floral display and only exotic flowers). More detailed information on the methods involved in quantification of natural habitat loss and relative exotic abundance is provided in a previously published study on the network structure of the studied plant–flower visitor communities (Grass *et al.* 2013).

#### ORIGIN OF DATA ON PLANT–FLOWER VISITOR INTERACTIONS

Our data set was based on recently published data on plant–flower visitor communities of our 17 study sites (Grass *et al.* 2013). In short, insect visitation to native and exotic plants was observed on a total of 70 different plant species flowering across the transects in the 17 sites. As a plant species could also be present in multiple study sites, we observed a total of 145 focal plants. Observations per focal plant consisted of four randomly allocated observation sessions of 20 min each ( $80 \text{ min} \times \text{focal plant}^{-1} \times \text{study site}^{-1}$ ). In most cases (~80%), and particularly when focal plants were herbaceous and grew in close proximity to another, we simultaneously observed multiple individuals per focal plant species. Furthermore, wherever possible, we observed different individuals at each of the four observation sessions. The floral abundance and the flower visitor assemblage of a focal plant were then calculated as the summed abundances and visitors of all observed individuals. All flower visitors were identified to the lowest taxonomic level possible and afterwards sorted into morphospecies, hereafter referred to as ‘species’ (139 visitor species in total). See Grass *et al.* (2013) for more information on survey of plant–flower visitor interactions, chosen focal plants for visitor observations and taxonomic resolution of flower visitor identification. For this study, we selected a subset of 131 focal plants (53 species; 39 native, 14 exotic), where every focal plant had received at least one visit, covering a total of 1434 flower visitor individuals. Note that in the following, we use the term ‘flower visitor community’ to refer to regionally (study area) and locally (within study sites) present visitor species and ‘flower visitor assemblage’ to refer to the specific subset of a local flower visitor community on a given focal plant.

#### MEASUREMENT OF FUNCTIONAL TRAITS OF FLOWER VISITORS

We measured the proboscis length, proboscis diameter and body length of up to 12 individuals per flower visitor species, depending on abundance. All measurements followed the methods described in Stang, Klinkhamer & van der Meijden (2006), except that we did not measure the length of the hind femur (Stang, Klinkhamer & van der Meijden 2006) but of the whole hind leg for calculation of body length. Measurements were undertaken under a dissecting microscope using an ocular micrometre and taken to the nearest 0.1 mm. In total, functional traits of 491 individuals including 131 visitor species were measured (measurements could not be undertaken for eight species due to damages, yet the 131 measured species represented 97.6% of all plant–flower visitor interactions in our data set; Table S1 and Appendix S1, Supporting Information). Correlations among mean values of visitor traits were weak to moderate ( $r = 0.16\text{--}0.43$ ).

#### QUANTIFICATION OF FUNCTIONAL DIVERSITY

Our aim was to understand changes in FD of flower visitors on plant species in differently disturbed study sites. We thus calculated flower visitor FD for each focal plant in a given study site,

based on the flower visitor assemblage of the plant. We used functional dispersion (FDis) as per Laliberté & Legendre (2010) to quantify the FD of a given flower visitor assemblage. Functional dispersion measures the mean distance of species’ trait values to the centroid of all species in trait space. The index is relatively unaffected by species richness, weighs trait values by species’ abundances and can be calculated for one or multiple traits (Laliberté & Legendre 2010). Information on abundance of flower visitors on a focal plant was derived from the number of visits of a species in 80 min of observations (see Methods above; Grass *et al.* 2013). We calculated multivariate FDis based on the dispersion of the three traits within the flower visitor assemblages on each of the 131 focal plants across our 17 study sites. Similarly, we calculated univariate FDis of each flower visitor trait on each plant.

We then used null model analysis to infer whether the observed flower visitor FD on a focal plant deviated from a model of random flower visitor assembly (Gotelli & Graves 1996; Mouchet *et al.* 2010). We first created a plant–flower visitor interaction matrix of the 131 focal plants and the 131 visitor species, based on the interaction frequencies of plants and their flower visitors. Secondly, to gain an expected null distribution of flower visitors on plants, we shuffled the entries of this matrix while keeping the marginal sums constant (10,000 randomizations). Thereby, we created random flower visitor assemblages on each focal plant per study site from the regional visitor pool while keeping visitor abundance per plant and study site constant, yet allowing visitor composition and richness to vary. Still, we are aware that this approach is limited in so far as it does not include flower visitors that were potentially present in the region but not recorded during visitor sampling (Pärtel, Szava-Kovats & Zobel 2011; Spasojevic & Suding 2012). We calculated the expected FDis of multivariate and univariate FDis as the mean of their FDis values over all randomizations, respectively, and then defined functional diversity (FD) as the deviance between observed and expected FDis values as  $FD_{\text{trait}} = FDis_{\text{trait\_observed}} - FDis_{\text{trait\_expected}}$  (Spasojevic & Suding 2012). Using the expected FDis values of the 10,000 randomizations, we inferred significant positive (overdispersion) or negative (underdispersion) departure from the null expectation at  $\alpha = 0.025$ .

#### STATISTICAL ANALYSES

As we investigated changes in flower visitor FD on the level of plants within study sites, our statistical analyses must account for the hierarchical design of our study. We therefore fitted linear mixed-effects models using R package ‘lme4’ (Bates, Maechler & Bolker 2012). As our design was not full factorial, that is not every plant species occurred in every study site, we fitted plant species identity and study site as separate random factors, corresponding to a partially crossed design. All models were fitted using restricted maximum likelihood (Bolker *et al.* 2009).

We generated separate global models for multivariate and univariate FD in flower visitor assemblages on focal plants across study sites. In each global model, we included plant origin (coded as a factor; 0 for native and 1 for exotic plants), natural habitat loss and relative exotic abundance as predictors, as well as the interaction of the two drivers. Here, it should be noted that relative exotic abundance therefore is a measure of the effect of exotic plants on flower visitors across study sites, whereas plant origin measures the response of individual visitors of the local flower visitor community to this plant trait within a given study site. We excluded the interactions of plant origin and the two drivers, as origin had no effect on changes in flower visitor FD with the two drivers. To account for differences in floral abundance of focal plants, we included the relative floral abundance (log-transformed) of each observed plant on the total floral abundance of all flowering plant species in a given study site (Grass *et al.* 2013). Here, we

used data from vegetation surveys to calculate means of floral abundance of plant species flowering at the time of the four observation sessions in a given study site. Including additional information on the number of observed floral units during surveys of plant–flower visitor interactions did not qualitatively affect the results and was therefore omitted for simplicity. Finally, although our measure of FD is largely unaffected by species richness, we included flower visitor richness (log-transformed) of assemblages on a given focal plant to investigate whether changes in FD went beyond those in visitor richness. In statistical notation, the full model read as:

1. FD measure  $\sim \log(\text{flower visitor richness}) + \log(\text{relative abundance of focal plant}) + \text{plant origin} + \text{natural habitat loss} \times \text{relative exotic abundance} + (1 | \text{plant species identity}) + (1 | \text{study site})$ .

To discern whether our measures of FD carried different (and thus potentially more ecologically relevant) information than species richness of flower visitors, we compared our results on changes in flower visitor FD to those on an analysis with visitor richness as response variable (log-transformed). Model structure was similar to that described above, except for excluding richness as predictor.

In this study, we assumed natural habitat and increasing relative floral abundance of exotic plants to be the main drivers of changes in flower visitor FD. However, flower visitor FD on a focal plant may not only be affected by habitat loss or exotic plant invasion, but can also be influenced by species-specific effects of the sampled plant species. For example, significantly underdispersed flower visitor FD on a given plant could result from habitat degradation, but also from functional constraints imposed by floral traits (e.g. a deep corolla tube; Pauw, Stofberg & Waterman 2009; Ibanez 2012). These and other co-evolutionary adaptations between plants and their flower visitors are often phylogenetically conserved (e.g. Rezende *et al.* 2007). We therefore conducted a series of statistical analyses to verify that increasing natural habitat loss and exotic plant abundance were the main drivers of changes in flower visitor FD (for detailed methods and results, see text and Tables S3 + S4 in Appendix S1). First, using permutational MANOVA, we analysed whether plant composition changed with increasing habitat loss or relative exotic abundance. Secondly, we included information on floral morphology (nectar holder depth, nectar holder width, size of the alighting place) in the linear mixed-effects models and compared effect sizes of habitat loss and relative exotic abundance to those of models without these covariates. Thirdly, to account for additional phylogenetically conserved traits and overall variation in the phylogenetic structure of plant communities across study sites, we included phylogenetic eigenvectors in the models and again compared effect sizes.

Information on changes in the FD of species communities along environmental gradients is insufficient if there is no indication of the reasons behind these changes (for example, a loss in groups of flower visitors with 'extreme' functional traits). Furthermore, even if FD is unaffected, the mean of a functional trait may change with increasing disturbance (with the variance around this mean remaining constant). We therefore quantified the direction of changes in flower visitor FD by investigating weighted mean values of flower visitor traits on each focal plant across the 17 study sites. Our approach resembled the calculation of community-weighted mean trait values as applied in other studies (e.g. Spasojevic & Suding 2012). Yet, similar to FD, we calculated the weighted mean of flower visitor traits on the level of plant species and not on the level of study sites. The structures of the mixed-effects models were similar to those on FD of flower visitors. However, we did not expect flower visitor richness or relative abundance of focal plants to affect the weighted mean of flower visitor traits, and including this information did not qualitatively affect our results. Consequently, we excluded these covariates

from the models. In addition, we used multivariate analysis to identify the most important groups of flower visitors driving the observed changes in trait values (detrended correspondence analysis; see Appendix S1 for detailed methods and results). Here, we focussed on compositional changes at the taxonomic scale of flower visitor families to reduce taxonomic complexity and achieve homogeneity in taxonomic resolution across morphospecies. We fitted natural habitat loss and relative exotic abundance on a two-dimensional ordination and used different coloration to visualize changes in weighted means of functional traits across flower visitor families.

For each linear mixed-effects model, we tested for spatial autocorrelation in the residuals (Moran's  $I$ ) in discrete distance classes of 4000 m (R package 'spdep'; Bivand *et al.* 2013). We found no evidence of spatial autocorrelation in any distance class (Moran's  $I$  close to zero and  $P > 0.094$  in all cases). Except for the categorical variable 'plant origin', all predictor variables were  $z$ -transformed (standardized to zero mean and unit variance) to facilitate the comparison of effect sizes (i.e. estimates of predictors). All statistical analyses were conducted in R 2.15.2 (R Development Core Team 2012).

## Results

Multivariate FD of flower visitors decreased with both global change drivers, that is along our gradients of natural habitat loss and increasing relative exotic plant abundance (Table 1, Fig. 1). Notably, effects of the two drivers were strong, although flower visitor richness was included in the model and generally had a positive effect on flower visitor FD (Table 1). Changes in multivariate FD thereby seemed to be mediated by complementary negative effects of the two drivers on different flower visitor traits (Fig. 2). FD in proboscis length decreased with natural habitat loss. FD in body length decreased with natural habitat loss and also with increasing relative exotic abundance (Table 1, Fig. 2). In contrast, natural habitat loss only had a marginal negative effect on FD in proboscis diameter (Table 1). While FD in proboscis length and FD in body length did not differ with plant origin, FD in proboscis diameter and multivariate FD were higher on exotic than on native focal plants (Table 1). In contrast to our expectation of interactive effects of the two global change drivers, we did not detect a significant interaction of natural habitat loss and relative exotic abundance in any model (Table 1). Importantly, in contrast to the observed changes in FD measures, species richness of flower visitors on plants was neither related to increasing natural habitat loss nor relative exotic abundance across study sites (Table S2 + Fig. S1).

The additional statistical analyses supported previous results on changes in flower visitor FD. Variation in plant species composition was not explained by increases in natural habitat loss across study sites ( $r^2 = 0.08$ ,  $F_{1,15} = 1.38$ ,  $P = 0.124$ ), and only little variation was related to relative exotic abundance ( $r^2 = 0.10$ ,  $F_{1,15} = 1.63$ ,  $P = 0.035$ ). Furthermore, including information on floral morphology of focal plants in the statistical models did not qualitatively or quantitatively alter previous results or substantially influence effect sizes of habitat loss and exotic plants



**Table 1.** Changes in multivariate and univariate functional diversity (FD) of flower visitor assemblages on native and exotic plants (131 focal plants) along gradients of loss of natural habitat and of relative exotic plant abundance (17 plant–flower visitor communities)

Source of variation	Estimate	Z	P
<b>Multivariate FD</b>			
Flower visitor richness	0.10	2.78	<b>0.0054</b>
Relative abundance	−0.092	−2.50	<b>0.013</b>
Plant origin	0.23	2.99	<b>0.0028</b>
Natural habitat loss	−0.14	−3.13	<b>0.0017</b>
Relative exotic abundance	−0.12	−2.18	<b>0.030</b>
Natural habitat loss × relative exotic abundance	−0.055	−1.37	0.17
<b>FD in proboscis length</b>			
Flower visitor richness	0.0077	0.28	0.78
Relative abundance	−0.034	−1.24	0.21
Plant origin	0.068	1.17	0.24
Natural habitat loss	−0.088	−2.50	<b>0.012</b>
Relative exotic abundance	−0.050	−1.20	0.23
Natural habitat loss × relative exotic abundance	−0.043	−1.39	0.16
<b>FD in proboscis diameter</b>			
Flower visitor richness	0.075	2.95	<b>0.0031</b>
Relative abundance	−0.059	−2.33	<b>0.020</b>
Plant origin	0.17	2.81	<b>0.0050</b>
Natural habitat loss	−0.053	−1.68	0.093
Relative exotic abundance	−0.047	−1.30	0.19
Natural habitat loss × relative exotic abundance	−0.017	−0.63	0.53
<b>FD in body length</b>			
Flower visitor richness	0.055	2.57	<b>0.010</b>
Relative abundance	−0.050	−2.36	<b>0.018</b>
Plant origin	0.088	1.74	0.082
Natural habitat loss	−0.063	−2.40	<b>0.016</b>
Relative exotic abundance	−0.068	−2.24	<b>0.025</b>
Natural habitat loss × relative exotic abundance	−0.022	−0.97	0.33

Effects were corrected for flower visitor richness and the relative floral abundance of a focal plant on the total floral abundance of all flowering plant species in a given study site. Predictors were standardized to zero mean and unit variance to ease the comparison of effect sizes. P values < 0.05 are highlighted in bold.

(Table S3). Finally, including information on the phylogenetic structure of focal plant communities in the models led to a decrease in the effect of habitat loss on FD in proboscis length, yet the overall negative effects of increasing natural habitat loss and relative exotic abundance on all other measures of functional diversity remained qualitatively and quantitatively similar (Table S4). In summary, effects of increasing natural habitat loss and relative exotic abundance were generally robust even when accounting for plant species-specific effects on flower visitor FD. These results supported our conclusion that habitat loss and exotic plant invasion were the most important drivers of losses in FD.

We also quantified changes in weighted mean values of flower visitor traits in order to assess the direction of changes in visitor FD. Proboscis length of flower visitors decreased with loss of natural habitat and relative exotic abundance (Table 2, Fig. S2) as well as with the interaction

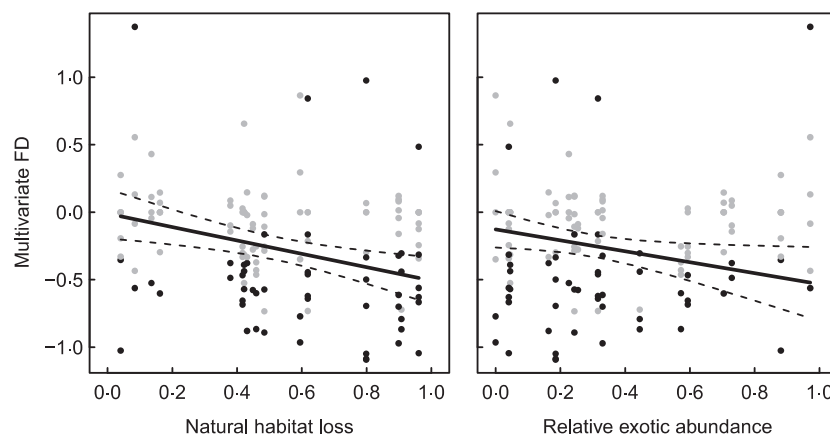
of the two drivers (Table 2, Fig. S3). Multivariate analysis indicated that the decrease in proboscis length was mainly driven by a lower number of Lepidoptera (e.g. Lyceanidae, Pieridae) and a higher abundance of Diptera (e.g. Tephritidae, Calliphoridae, Sciomyzidae) in sites with high habitat loss or relative exotic abundance (Fig. S4). Proboscis diameter increased with loss of natural habitat (Table 2, Fig. S2), which again seemed to be driven by increases in particular Diptera families (e.g. Tephritidae, Sarcophagidae, Calliphoridae; Fig. S4). Neither natural habitat loss nor relative exotic abundance had an effect on the mean body length of flower visitors, indicating that the loss of FD in body length resulted from decreased variance in body length, or the loss of specifically sized flower visitors (Table 2, Figs S2 + S4). Finally, we found no differences in the weighted means of flower visitor traits between native and exotic plant species (Table 2).

## Discussion

We found decreasing multivariate FD of flower visitors along both environmental gradients, with complementary negative effects of natural habitat loss and increasing relative exotic plant abundance. Importantly, responses of flower visitor FD to the two global change drivers were trait specific and thereby complementary. While natural habitat loss led to a decline of FD in proboscis length and body length, FD in body length also decreased with exotic plant abundance.

### MULTIVARIATE FD OF FLOWER VISITORS

Although pollinator FD can be closely related to pollination processes and the stability of plant–pollinator communities (Fontaine *et al.* 2006; Albrecht *et al.* 2012), effects of ecosystem disturbance on pollinator FD are poorly understood. Here, we present the first study on the effects of multiple drivers of global change on flower visitor FD and demonstrate that both the loss of natural habitat and invasions by exotic plants have negative effects on multivariate FD. There are numerous studies that have demonstrated a loss in species richness and abundance of pollinators or flower visitors in disturbed or invaded habitats (Kremen, Williams & Thorp 2002; Potts *et al.* 2010; Montero-Castaño & Vilà 2012 and references therein). Our study substantially contributes to these studies as we demonstrate that flower visitor FD decreased independently from flower visitor richness. Here, it should be noted that our chosen measure of flower visitor FD, functional dispersion, naturally covers only some facets of FD, whereas other measures (e.g. functional richness; Schleuter *et al.* 2010) may be more closely related to flower visitor richness. However, in contrast to the example functional richness, functional dispersion allowed us to measure the functional differentiation of flower visitors in an abundance-weighted manner. While flower visitor richness has been shown to be a good predictor of pollination processes and plant reproductive output (e.g. Garibaldi *et al.* 2013), it may



**Fig. 1.** Loss in multivariate FD of flower visitors with increasing loss of natural habitat (left panel) and relative abundance of exotic plants (right panel) in a heterogeneous subtropical landscape. Calculation of multivariate FD was based on three visitor traits (proboscis length, proboscis diameter and body length). Shown are effects of drivers from a linear mixed-effects model (solid lines) and 95% confidence intervals (dashed lines). Effects are corrected for other covariates in the model. Grey and black points show the underlying raw data for each flower visitor assemblage on a given focal plant, with black points indicating significant deviation from null model distribution.

therefore not cover all facets of flower visitor FD that are relevant to pollination processes and can promote plant-pollinator community stability. Our findings also suggest that the FD of flower visitors may already have declined in disturbed habitats in which visitor richness is still unaffected. For example, the meta-analyses by Winfree, Aguilar & LeBuhn (2009) and Montero-Castaño & Vilà (2012) have shown that pollinator richness and abundance are almost unaffected by moderate habitat loss (e.g. 50% natural habitat cover remaining) and only significantly decrease when habitat loss is extreme (e.g.  $\leq 5\%$  natural habitat cover remaining). In our study, flower visitor FD was already lower than expected at moderate levels of habitat loss (Figs 1+2), while flower visitor richness was neither related to increasing natural habitat loss nor relative exotic abundance.

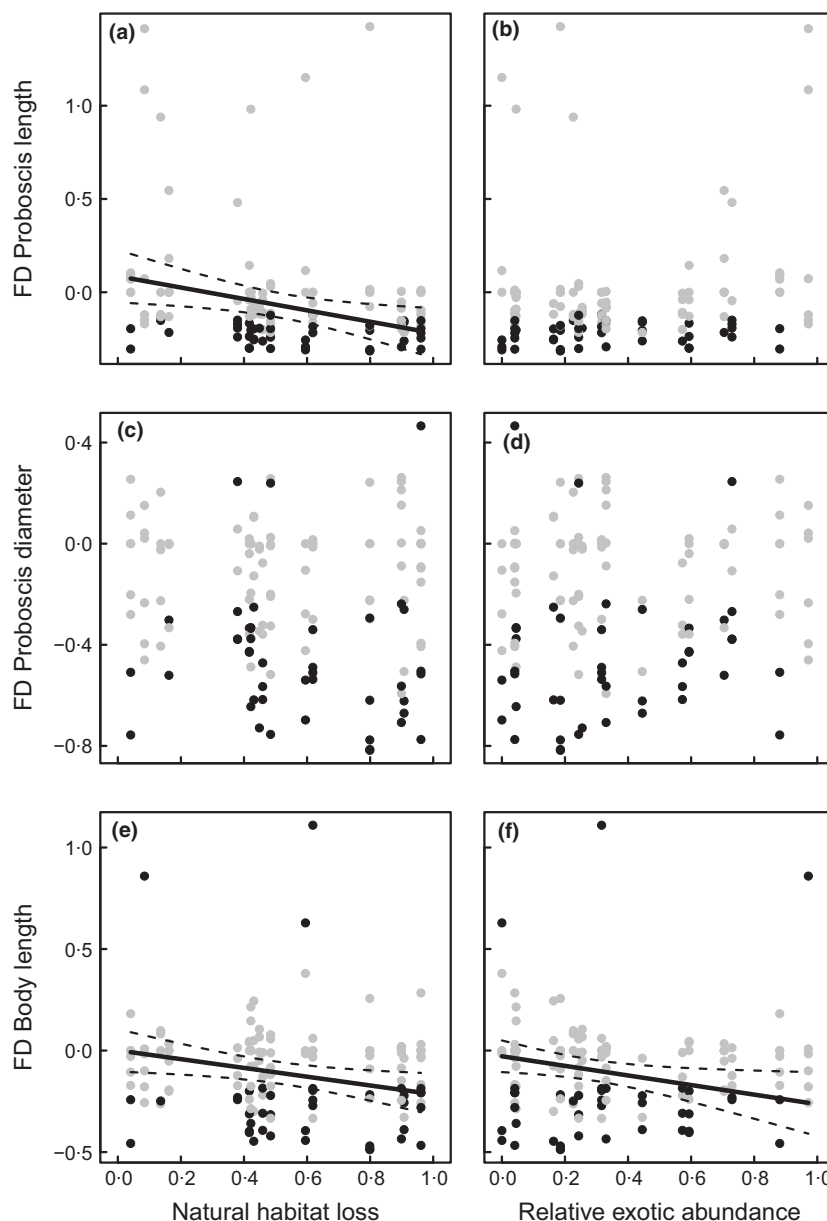
In addition to the negative effects of natural habitat loss, we detected a reduction in multivariate flower visitor FD with increasing relative abundance of exotic plants. Exotic plants may favour generalized flower visitors that are functionally similar, highly abundant and strong competitors (Richardson *et al.* 2000; Johnson & Steiner 2000; Montero-Castaño & Vilà 2012). Low FD of flower visitors in sites with high relative exotic abundance thus may be attributed to a loss in specialized visitors with 'extreme' functional traits and a change towards flower visitor assemblages with a more uniform trait composition. Particularly, the dominance of a single or few exotic plant species in invaded habitats may severely diminish the diversity of floral resources and ultimately reduce native plant and related pollinator diversity (Cox & Elmqvist 2000; Traveset & Richardson 2006). Accordingly, we found negative correlations between relative exotic abundance and the Shannon diversity ( $r = -0.53$ ;  $n = 17$ ;  $P = 0.030$ ) and Pielou's evenness ( $r = -0.55$ ;  $n = 17$ ;  $P = 0.026$ ) of plant communities in our study system. However, neither plant diversity nor plant evenness were significant predictors of flower

visitor diversity when used in addition or as substitutes for relative exotic abundance in our models (data not shown). Consequently, dominance effects of exotic plants did not fully explain reductions in flower visitor FD. Other aspects of plant invasions (e.g. lag times in the establishment of interactions with flower visitors) may have additionally reduced visitor FD. Interestingly, we also found higher multivariate FD of flower visitors on exotic plants than on native plants. This finding seems counterintuitive, yet it can be explained by the design of our study. While relative exotic abundance was a measure of the effect of exotic plants on flower visitor FD across study sites, plant origin is a plant trait that affected local flower visitors within study sites. Consequently, while high relative abundance of exotic plants in many cases led to a reduction in the FD of flower visitors, the remaining visitor assemblage within a given study site still could show higher FD on exotic plants than on natives.

Importantly, although natural habitat loss and exotic plant abundance were comparable in generally reducing flower visitor FD, the two drivers affected different visitor traits. This illustrates the usefulness of separately investigating responses of individual flower visitor traits to multiple drivers of global change (see also Williams *et al.* 2010). Different responses among visitor traits to natural habitat loss and exotic plant abundance may also explain the absence of interactive (e.g. synergistic) effects of the two global change drivers on univariate and multivariate FD. In the following, we disentangle the detected changes in multivariate FD of flower visitors by separately investigating changes in FD of individual traits.

#### TRAIT-SPECIFIC CHANGES IN FD OF FLOWER VISITORS

Loss of natural habitat led to a reduction of FD in proboscis length of flower visitors. Investigating changes in mean



**Fig. 2.** Changes in FD in three flower visitor traits with increasing loss of natural habitat and relative exotic plant abundance. Natural habitat loss negatively affected FD in proboscis length of flower visitors, which was unaffected by relative exotic abundance (panels a+b). FD in proboscis diameter did not change along both gradients (c+d). FD in body length of flower visitors decreased with natural habitat loss as well as increasing relative exotic abundance (e+f). Shown are effects of drivers from linear mixed-effects models (solid lines) and 95% confidence intervals (dashed lines). Effects are corrected for other covariates in models. Grey and black points show the underlying raw data for each flower visitor assemblage on a given focal plant, with black points indicating significant deviation from null model distribution.

proboscis length suggested that this reduction was mainly caused by a loss in long-tongued butterflies. Accordingly, multivariate analysis showed that butterfly families were generally absent from study sites with high degree of habitat loss. Loss of natural habitat may negatively affect butterflies via a loss in habitat connectivity and a reduced abundance of suitable host plants (Woodhall 2005; Brückmann, Krauss & Steffan-Dewenter 2010). Similarly, we found negative effects of increasing relative exotic abundance on the proboscis length of flower visitors and an even stronger negative effect of the two drivers when these acted in synergy. In addition to the loss of long-tongued flower visitors with habitat loss, exotic plants may have attracted abundant generalist visitors with short- to medium-sized proboscides (e.g. the native pollinator *Apis mellifera*). Consequently, the average proboscis length of

flower visitors was strongly reduced in study sites with low remaining natural habitat cover and a high abundance of exotic plants. This finding confirms the prediction that interactive effects between habitat loss and exotic plant invasions may particularly threaten specialized native species and their interactions (Didham *et al.* 2007; Potts *et al.* 2010). Particularly, long-tongued flower visitors are often important agents in specialized pollination systems (e.g. Johnson & Steiner 2000; Pauw, Stofberg & Waterman 2009). Reduced abundance of long-tongued flower visitors in disturbed habitats may negatively affect the pollination of plant species with deep nectar holders (Pauw, Stofberg & Waterman 2009; Stang *et al.* 2009).

Similarly to the changes in proboscis length, we recorded shifts in the composition of proboscis diameters with natural habitat loss. Flower visitors with the widest proboscides

**Table 2.** Changes in weighted mean trait values of flower visitor assemblages on native and exotic plants (131 focal plants) with natural habitat loss and increasing relative exotic abundance (17 plant–flower visitor communities)

Source of variation	Proboscis length			Proboscis diameter			Body length		
	Estimate	Z	P	Estimate	Z	P	Estimate	Z	P
Plant origin	0.18	0.82	0.41	−0.013	−0.29	0.77	0.98	0.90	0.37
Natural habitat loss	−0.26	−2.92	<b>0.0035</b>	0.056	2.59	<b>0.0097</b>	−0.42	−0.90	0.37
Relative exotic abundance	−0.20	−2.01	<b>0.045</b>	0.0015	0.06	0.95	−0.35	−0.66	0.51
Natural habitat loss × relative exotic abundance	−0.15	−2.05	<b>0.041</b>	−0.018	−0.95	0.34	−0.17	−0.41	0.68

Predictors were standardized to zero mean and unit variance. P values < 0.05 are highlighted in bold.

were mostly flies, for example species of the genera *Didacus* (Tephritidae) and *Psilodera* (Acroceridae), which may prevail in disturbed habitats. Accordingly, Calliphoridae and Sarcophagidae were most abundant in study sites with low remaining natural habitat cover. Interestingly, the flower visitor assemblages of exotic plants had an overall higher FD in proboscis diameter than the assemblages on native plants. As proboscis diameter was the only functional trait in which flower visitor FD differed between native and exotic plants, this trait likely is also responsible for the higher multivariate FD on exotics. The floral morphology of the exotic plants in our study may have imposed fewer constraints on local visitor assemblages than their native competitors in the same local community. Some abundant native plant species may have particularly limited access of visitors with wide proboscides. Specifically, native plant species with an otherwise generalized pollination syndrome (e.g. plants of the Asteraceae family) often had a narrow nectar holder (Stang *et al.* 2009).

Functional diversity in body length decreased with natural habitat loss, yet mean body length was unaffected. Thus, habitat loss seemed to decrease the variance in differently sized flower visitors, and in particular seemed to negatively affect small (Greenleaf *et al.* 2007) and comparably large (e.g. butterflies; Brückmann, Krauss & Steffan-Dewenter 2010) flower visitors. Moreover, complementing the effects of natural habitat loss, FD in the body length of flower visitors decreased with increasing relative exotic abundance. As the diversity of plant resources and of pollinators are strongly linked to one another (Potts *et al.* 2003), particularly the dominance of floral resources by a single or few highly abundant exotic plant species (e.g. *L. camara* or *A. mearnsii*) may have reduced the FD in body length (Traveset & Richardson 2006; Potts *et al.* 2010). For example, invaded study sites in which the butterfly-pollinated *L. camara* was most abundant supported relatively high abundances of butterflies (given that natural habitat cover was sufficient, personal observation). Contrastingly, Hymenoptera (e.g. the native honeybee *Apis mellifera*) mainly dominated within study sites with high abundance of *A. mearnsii*. Consequently, plant–flower visitor communities with high relative abundance of single or few exotic plant species may lack those small or large flower visitors that by functional complementary promote

pollination of the remaining native plant species (Blüthgen & Klein 2011; Albrecht *et al.* 2012).

#### LIMITATIONS OF OUR STUDY

An obvious limitation of our study is that we did not investigate the species-specific differences in pollination efficiency of flower visitor species (Herrera 1987; King, Ballantyne & Willmer 2013). Therefore, it remains elusive whether the detected losses in flower visitor FD also resulted in reduced reproductive output, that is seed or fruit set, of plant species. However, with regard to studies emphasizing the importance of pollinator FD for the reproductive output of plant species and the stability of plant–pollinator communities (Fontaine *et al.* 2006; Albrecht *et al.* 2012), our results strongly suggest that at least some specialized plant species may suffer from reduced pollination in study sites with low natural habitat cover or high relative abundance of exotic plants. One example is the loss of long-tongued flower visitors with the additive and interactive effects of both drivers. The remaining visitors with short proboscides can be inefficient pollinators or even act as pollen thieves of plants with deep nectar holders (e.g. Hargreaves, Harder & Johnson 2012). In turn, these plants may show reduced levels of cross-fertilization, with consequences for the ratio of different flower morphs in a population (Simón-Porcar, Santos-Gally & Arroyo 2014) or co-evolutionary processes (Pauw, Stofberg & Waterman 2009). Consequently, the loss of flower visitor FD in this subtropical landscape calls for future studies that investigate the consequences for plant reproductive output and the stability of plant–pollinator communities.

#### Conclusions

Here, we show a reduction in the FD of flower visitors with increasing magnitude of two major drivers of global change, that is loss of natural habitat and exotic plant invasions. Our results show that these drivers have complementary negative effects when they affect different functional traits of flower visitors. This result would have been overlooked in a single-driver study. Furthermore, we found that decreases in the FD of flower visitors went



beyond those in species richness of flower visitors and that visitor richness was not related to either of the two drivers. While flower visitor richness in general thus often is a good predictor of pollination processes (e.g. Garibaldi *et al.* 2013), it does not necessarily cover all relevant facets of flower visitor FD. We suggest that investigating patterns in flower visitor FD along environmental gradients substantially improves understanding and predictions of effects of global change on pollination processes, particularly when multiple visitor traits and drivers of global change are considered.

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## Data accessibility

Data deposited in the Dryad repository: <http://doi.org/10.5061/dryad.fb96h> (Grass *et al.* 2014).

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## Supporting Information

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

### Appendix S1. Methods and results.

**Table S1.** Mean trait values and abundance of 131 flower visitor species (species + morphospecies) in 17 plant-flower visitor communities.

**Table S2.** Effects of natural habitat loss and relative exotic abundance on species richness of flower visitors.

**Table S3.** Plant traits that were included as additional covariates in statistical models to predict changes in flower visitor FD with natural habitat loss and relative exotic abundance.

**Table S4.** Effects of natural habitat loss and relative exotic abundance before and after correcting for effects of phylogenetic relatedness among plant species.

**Fig S1.** Species richness of flower visitors on plant species along gradients of increasing natural habitat loss and relative exotic abundance in a subtropical landscape (observed on 131 plant species across 17 plant-flower visitor communities).

**Fig S2.** Weighted mean trait values of flower visitors along increasing gradients of loss of natural habitat and relative exotic plant abundance in a subtropical heterogeneous landscape (observed on 131 plant species across 17 plant-flower visitor communities).

**Fig S3.** Changes in weighted mean proboscis length of flower visitors with increasing natural habitat loss and relative abundance of exotic plant species across study site.

**Fig S4.** Ordinations of the detrended correspondence analysis (DCA) on family composition of flower visitors.