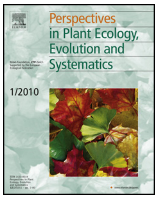
Perspectives in Plant Ecology, Evolution and Systematics xxx (2013) xxx–xxx

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Research article

Plant functional traits and community assembly along interacting gradients of productivity and fragmentation

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ARTICLE INFO

Article history:
Received 15 February 2012
Received in revised form 10 July 2013
Accepted 11 August 2013
Available online xxx

Keywords:
Connectivity
Drought-stress
Habitat filtering
Limiting similarity
Null models
Plant height
Seed mass
Seed number
Specific leaf area (SLA)

ABSTRACT

Quantifying the association of plant functional traits to environmental gradients is a promising approach for understanding and projecting community responses to land use and climatic changes. Although habitat fragmentation and climate are expected to affect plant communities interactively, there is a lack of empirical studies addressing trait associations to fragmentation in different climatic regimes.

In this study, we analyse data on the key functional traits: specific leaf area (SLA), plant height, seed mass and seed number. First, we assess the evidence for the community assembly mechanisms habitat filtering and competition at different spatial scales, using several null-models and a comprehensive set of community-level trait convergence and divergence indices. Second, we analyse the association of community-mean traits with patch area and connectivity along a south–north productivity gradient.

We found clear evidence for trait convergence due to habitat filtering. In contrast, the evidence for trait divergence due to competition fundamentally depended on the null-model used. When the null-model controlled for habitat filtering, there was only evidence for trait divergence at the smallest sampling scale (0.25 m × 0.25 m). All traits varied significantly along the S–N productivity gradient. While plant height and SLA were consistently associated with fragmentation, the association of seed mass and seed number with fragmentation changed along the S–N gradient.

Our findings indicate trait convergence due to drought stress in the arid sites and due to higher productivity in the mesic sites. The association of plant traits to fragmentation is likely driven by increased colonization ability in small and/or isolated patches (plant height, seed number) or increased persistence ability in isolated patches (seed mass).

Our study provides the first empirical test of trait associations with fragmentation along a productivity gradient. We conclude that it is crucial to study the interactive effects of different ecological drivers on plant functional traits.

Introduction

Habitat fragmentation, climate change, and their interactive effects have been highlighted as the most important drivers of diversity loss and of shifts in species composition in plant communities (Sala et al., 2000; Fahrig, 2003; Travis, 2003; Opdam and Wascher, 2004; Thuiller et al., 2005; Parmesan, 2006; Jeltsch et al., 2011). Drastic shifts in community composition and structure were especially predicted for species range margins and ecotones that represent transition zones between different ecosystems and different climatic regimes (Allen and Breshears, 1998; Hampe and Petit, 2005; Thuiller et al., 2008).

A promising approach for understanding and for ultimately projecting community responses to environmental changes is the quantification of the association between plant functional traits and environmental conditions (Lavorel and Garnier, 2002;

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http://dx.doi.org/10.1016/j.ppees.2013.08.002

McGill et al., 2006; Jeltsch et al., 2008). So far, numerous studies adopted the framework of trait-based ecology to address community assembly processes and changes of plant functional traits along climatic gradients in different continents and at scales ranging from regional to global (Díaz and Cabido, 1997; Fonseca et al., 2000; Wright et al., 2004; Westoby et al., 2002; Cornwell and Ackerly, 2009). The link between plant functional traits and habitat fragmentation was primarily studied in temperate European ecosystems focussing on forest herbs (Dupré and Ehrlén, 2002; Kolb and Diekmann, 2005; Hérault and Honnay, 2005), semi-natural grasslands (Lindborg, 2007; Lindborg et al., 2012; Marini et al., 2012; Purschke et al., 2012) and urban ruderal communities (Schleicher et al., 2011). However, little is known on the response of plant functional traits to habitat fragmentation in other climatic regimes (Chust et al., 2006) and on the interacting effects of climate and fragmentation on functional trait distributions in plant communities.

Classical community assembly theory encompasses two potentially opposing processes that affect the distribution of functional traits within and among communities. First, as species distributions are often shaped by environmental conditions, co-occurring species are likely to experience and to be functionally adapted to the same abiotic environment. This process is known as "habitat filtering" and is expected to result in trait convergence among co-occurring species (Cornwell and Ackerly, 2009). Second, as species with similar functional traits are assumed to experience substantial niche overlap, interspecific competition is expected to preferentially exclude species with high trait similarity and thus results in trait divergence within communities (MacArthur and Levins, 1967; Stubbs and Wilson, 2004; Kraft et al., 2008). The effects of these opposing processes may vary with the spatial scale, with habitat filtering being predominant on comparably large spatial scales with substantial environmental variation, while interspecific competition might be more important at small spatial scales, where plants actually compete for resources (Kraft and Ackerly, 2010). In addition to its influence on trait distributions within communities, habitat filtering may also cause shifts in community-mean trait values along environmental gradients (Ackerly and Cornwell, 2007; Cornwell and Ackerly, 2009).

In this study, we investigate plant functional trait distributions in a fragmented landscape that encompasses a steep south–north environmental gradient at the transition zone between desert and Mediterranean ecosystems (Giladi et al., 2011). Our study area in the Southern Judean Lowlands (SJL), Israel, consists of discrete habitat patches of natural vegetation embedded in a matrix that is used for intensive agriculture (Yaacobi et al., 2007; Gavish et al., 2011; Giladi et al., 2011). The natural scrubland and grassland vegetation features high species richness and a high proportion of annual plant species. Natural habitat patches of different sizes and degrees of isolation occur everywhere along the S–N gradient, such that habitat fragmentation is not confounded with the environmental gradient. Therefore, this landscape is well suited to study the interacting effects of fragmentation and environmental conditions on plant functional traits. In previous studies conducted in the same landscape, we found that the relative importance of fragmentation and the position along the S–N gradient for species richness varies with spatial scale (Giladi et al., 2011) and we assessed the role of habitat connectivity for regional community dynamics (May et al., 2013). Here, we focus on the interactive effects of fragmentation and environmental gradients on the distribution of plant functional traits within and among communities.

Hypotheses on the association of plant functional traits with fragmentation are based on island biogeography and metapopulation theories (MacArthur and Wilson, 1967; Hanski, 1999). The presence of a species in a given patch within a fragmented landscape depends on its ability to (a) colonize the patch, and (b) persist in a patch once present. Persistence can be either assured by positive long-term population growth in the focal patch or by the input of sufficient propagules from neighbouring patches, which is known as rescue effect (Brown and Kodric-Brown, 1977). As the challenge of colonization increases with patch isolation, we expect that plants with traits that favour colonization will be disproportionally over-represented in isolated patches (Dupré and Ehrlén, 2002). As the rescue-effect will be most important for small populations in small patches, we additionally expect that plants with traits that favour colonization will be disproportionally over-represented in small patches as well (Hanski, 1999; Dupré and Ehrlén, 2002). Analogously, as extinction risk increases with a decreasing patch size, the challenge of persistence also increases and therefore we expect that plants with traits favouring persistence will be disproportionally over-represented in smaller patches. Predictions for the associations between specific traits, patch isolation and patch area are provided in detail in Table 1.

The importance of various functional traits for species persistence may vary along environmental gradients. In our study area, increasing precipitation and increasing plant density from south to north indicate that there is a shift from high drought-stress in the south to higher productivity and thus higher intensity of above-ground competition in the north (Giladi et al., 2011). Therefore, our hypotheses on the response of plant functional traits to patch area rely on the premise that species persistence in the south will mainly depend on a species' ability to cope with drought-stress, while in the north it will depend on the ability to avoid competitive exclusion (Grime, 2001). Considering the interactive effects of patch area and the position along the S–N gradient, we therefore predict that in the arid sites trait adaptation to drought-stress is higher in small than in large patches, while in the mesic sites adaptation to competition is higher in small than in large patches (Table 1).

For this study we sampled five key plant functional traits – specific leaf area (SLA), canopy height, seed-release height, seed mass and seed number (Westoby et al., 2002; Cornelissen et al., 2003). This study is organized in two main conceptual parts: In the first one, we assess trait convergence and trait divergence within plant communities to answer the following specific questions with respect to community assembly processes: (1a) Are plant communities in the SJL structured by habitat filtering? (1b) Is there evidence for trait divergence among co-occurring species as expected from the effects of interspecific competition? (1c) Does the evidence for habitat filtering and/or competition in trait distributions vary with spatial scale? (1d) Does the strength of habitat filtering and/or competition vary along the S–N gradient or with fragmentation? In the second part we focus on the issue of plant trait distributions along the S–N and fragmentation gradients. More specifically we investigate: (2a) How do community-mean traits values change along the S–N gradient? (2b) Are community-mean traits values associated with fragmentation? (2c) Does the association of community-mean traits with fragmentation change along the S–N gradient?

Methods

Study area

The study area is located in the Southern Judean Lowlands (SJL), Israel (31°24′–31°41′N; 34°46′–34°52′E) (Fig. 1). This region represents a transition zone between desert and Mediterranean ecosystems with a sharp increase in precipitation from south to north. The study area is characterized by a typical semi-arid climate, with short mild winters and long, dry and hot summers. Mean

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Table 1
Specific predictions of plant functional trait responses to climate, fragmentation and the interactive effects of climate and fragmentation. The predictions always refer to the expected response of community-mean traits to environmental drivers. General theory and hypotheses on trait–environment relationships are provided in the main text.

Environmental driver	Prediction	Rationale	References
Climate			
	Arid sites: Low SLA Low seed mass High seed number	Adaptation to drought-stress and bet-hedging	Westoby et al. (2002), Leishman et al. (2000), Venable and Brown (1988)
	Mesic sites: High SLA High plants High seed mass	Adaptation to above-ground and seedling competition	Westoby et al. (2002), Grime (2006), Metz et al. (2010)
Fragmentation			
	Small and isolated patches: High seed release height High seed number	Dispersal distance and colonization ability increase with seed release height and seed number	Clark et al. (1999), Dupré and Ehrlén (2002), Tackenberg et al. (2003), Thomson et al. (2011)
Climate × fragmentation			
	Small and arid patches: Very low SLA Very low seed mass Very high seed number	High extinction risk in small patches requires high degree of adaptation to drought-stress	
	Small and mesic patches: Very high SLA Very high seed mass Very high plants	High extinction risk in small patches requires high degree of adaptation to competition	

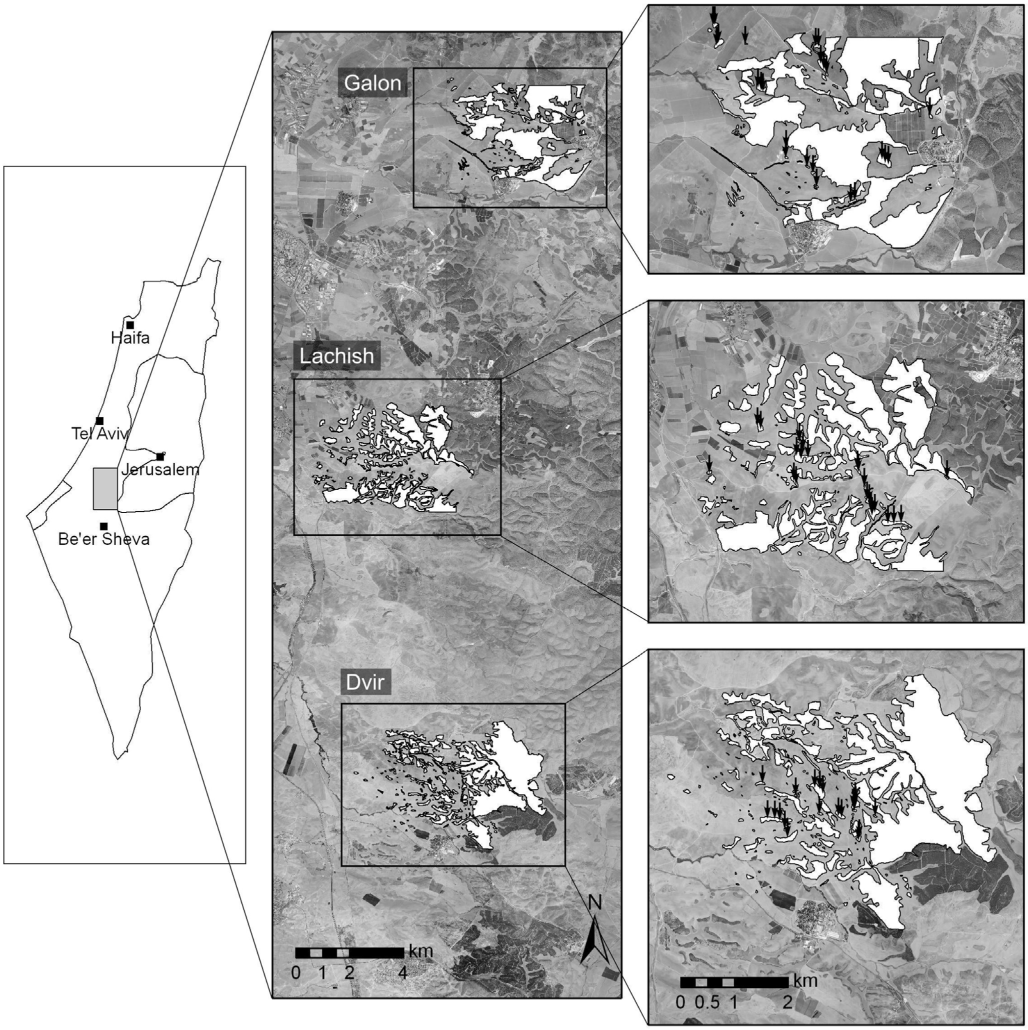

Fig. 1. Maps of the Southern Judean Lowlands. The left panel shows the location of the study area in Israel. The middle panel shows the arrangement of the land units along the south–north gradient. The three panels on the right show all digitized patches with natural vegetation in each land unit (in white). Arrows indicate patches where vegetation surveys were conducted and for which community-level trait indices were derived.

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Table 2
Climate and soil data for each land unit in the Southern Judean Lowlands. Precipitation data are from the Israeli Meteorological service data base for the years 1975–2009. Data were collected from weather stations that are within 5 km of the field sites. Temperature data are long-term averages from Goldreich (2003). The wettest month was December, January or February (with 2 exceptions where November was the wettest).

Land unit	Precipitation [mm]			Temperature [°C]			Soil properties	
	Annual mean	Mean driest month	Mean wettest month	Annual mean	Mean coldest month	Mean hottest month	Field capacity (% volumetric water content)	Soil organic matter [mol C/kg soil]
Galon	430 ± 149	0	154 ± 64	19	10	25	74.6 ± 5.3	7.8 ± 1.2
Lachish	395 ± 136	0	146 ± 60	19	10	25	63.8 ± 6.6	6.3 ± 1.0
Dvir	291 ± 118	0	110 ± 47	19	11	26	55.1 ± 4.1	6.0 ± 1.0

annual temperature is 19 °C (12 °C in January and 26 °C in August) throughout the study area. Mean annual precipitation, which is almost exclusively restricted to October until March, increases from 300 mm in the south to 450 mm in the north over a distance of 30 km only (Table 2). This increase in precipitation results in substantial increases in plant density, plant species richness (Giladi et al., 2011), vegetation biomass (Schmidt and Gitelson, 2000) and in considerable changes in floral community composition (Kadmon and Danin, 1997, 1999).

For thousands of years the landscape has been used for sheep and goat grazing and small scale subsistence farming (Naveh and Dan, 1973; Ackermann et al., 2008). Intensified agriculture in the last decades reshaped the landscape into a patch-matrix mosaic, with clear boundaries between semi-natural habitat and agricultural matrix (Fig. 1) (Yaacobi et al., 2007; Gavish et al., 2011; Giladi et al., 2011). Historical aerial photographs showed that the distribution of natural habitat patches in the landscape has remained relatively constant during the last 60 years (I. Giladi, unpublished data). Today the natural vegetation patches experience sheep grazing on the south and cattle grazing in the north of the SJL (Rotem, 2012).

The main vegetation types are characterized as semi-steppe batha (Mediterranean scrubland) and grassland (Giladi et al., 2011). The most dominant perennial species are the dwarf shrub *Sarcopoterium spinosum* in the batha vegetation and the tussock grasses *Hyparrhenia hirta* and *Hordeum bulbosum* in the grassland. Plant communities are characterized by a high species richness of 83 ± 17 species (mean ± standard deviation, $n = 81$) at the 15 m × 15 m plot scale, and by a high proportion of annual species throughout the study region, accounting for 67% of all species. The most common annual species are *Avena sterilis*, *Anagallis arvensis*, *Linum strictum*, *Urospermum picriodes*, and *Plantago afra* (Giladi et al., 2011).

In this study we exclusively focus on annual plant species in order to control for a potentially varying representation of plant species' life forms in the sampled communities. We sampled plant traits and conducted vegetation surveys in three land units, called Dvir, Lachish and Galon arranged along a S–N gradient (Fig. 1, Table 2). Due to the substantial increase in mean annual precipitation, we will refer to Dvir as the "arid" and to Galon as the "mesic" end of the S–N gradient. Each land unit (4 km × 6 km) includes 70–170 natural vegetation patches of different sizes ranging from continuous (>100 ha) to very small patches (<100 m^2). We used rectified aerial photographs (pixel size = 1 m^2) to identify and digitize all the patches of natural vegetation within each of the three land units. The digitized map was stored as vector-based format in a Geographical Information System (GIS) platform (ArcGIS^{TM}; ESRI) and used for the calculations of patch area and connectivity.

Patch connectivity

The connectivity of a patch correlates with the probability of seed dispersal into that patch from other patches in the landscape (Moilanen and Nieminen, 2002). According to previous studies, we assumed that patch connectivity increases with the number and area of neighbouring patches and decreases with patch-to-patch distances (Hanski, 1999; Hovestadt and Poethke, 2005). However, in previous studies patch-to-patch distances were usually measured between patch centroids or between patch edges (reviewed in Moilanen and Nieminen, 2002). These may be reasonable approximations if the distances between patches are much larger than the patch extents, but if patch extents and inter-patch distances are of similar order of magnitude, as in our landscape (Fig. 1), considering patch shapes and orientations may much better reflect the functional connectivity (i.e. the probabilities of seed dispersal) among patches (Chipperfield et al., 2011). Therefore, we use a connectivity index that considers patch shapes and orientations explicitly (May et al., 2013). In contrast to May et al. (2013), we standardize patch connectivities by patch areas in order to avoid collinearity between these two fragmentation variables. A detailed description of the calculation of patch connectivities is provided in the supplementary material.

Vegetation sampling

We established 80 vegetation sampling plots of the size 15 m × 15 m within 40 patches of natural vegetation (26, 29 and 25 plots in 12, 16 and 12 patches within Dvir, Lachish and Galon, respectively). Each 15 m × 15 m plot included 3, 6 and 12 subplots of the sizes 5 m × 5 m, 1 m × 1 m and 0.25 m × 0.25 m, respectively (Giladi et al., 2011). In our study landscape habitat fragmentation and patch sizes are confounded with an east to west gradient. However, by a careful choice of patches to be sampled, we were able to avoid these confounding effects in our sampling (Fig. 1).

The number of plots placed within each patch varied according to patch area and ranged between one and seven plots. All annual plant species within each sampling plot were recorded during the peak of the growing season between early March and early April in 2008 and 2009. In 2009 we recorded plant density as well by counting all individuals within the 12 small sampling subplots of the size 0.25 m × 0.25 m in each 15 m × 15 m plot (Giladi et al., 2011).

In 77 of the plots we collected soil samples. Each soil sample consisted of a mixture of three 300 g sub-samples taken at a depth of 10 cm from three positions within a plot. These samples were later used for measurements of field capacity and organic matter content using standard soil analysis methods (Carter and Gregorich, 2007). Organic matter content was determined by the loss of ignition procedure (LOI). Field capacity was determined by a simple gravimetric procedure.

The 40 patches sampled include five patches of continuous habitat, each with an area of more than 35 ha, while all other patches are smaller than 5 ha. We do not expect that large areas of continuous natural habitat depend on propagule immigration from much smaller neighbouring patches (Giladi et al., 2011). Therefore,

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connectivity indices were only calculated for patches smaller than 5 ha.

Trait measurements

From a “core list” of plant functional traits we chose two vegetative and three regenerative traits, which were proposed to reflect plant strategies along environmental gradients (Weiher et al., 1999; Westoby et al., 2002). As vegetative traits we measured canopy height (CH) [cm] and specific leaf area (SLA) [mm^2/mg], which was derived by dividing fresh leaf area by leaf dry mass. As regenerative traits we recorded seed release height (SRH) [cm], the seed mass of one seed (SM) [mg] and the seed number (fecundity) of one individual (SN). Seed mass was measured after removing any seed appendages (Cornelissen et al., 2003).

Trait sampling was conducted in March and April 2009 and 2010, and measurements followed the standard protocols suggested by Cornelissen et al. (2003) and Kleyer et al. (2008). Accordingly, CH and SRH were measured for 25 individuals and SLA, SM and SN for 10 individuals per species. For SLA measurements we sampled two fresh, healthy and light exposed leaves per plant. If a species has different types of leaves, we collected two leaves from each type. For seed mass we used at least 10 ripe seeds of each plant and 10 seeds per type, if the species produces different types of seeds. We estimated seed number (fecundity) by calculating the product of the number of fruits/infructescences per individual (counted in 10 plant individuals) and the average number of seeds per fruit/infructescences (counted in two fruits or infructescences, respectively, collected prior to any dispersal).

Usually, trait measurements were conducted in one well-established population. However, for rare species and species with very low population density, we pooled data from several populations to attain the sample sizes mentioned above. Accordingly, our results always refer to interspecific trait variation and we do not address intraspecific trait variation in this study. For 12 species we supplemented our data for seed mass with measurements taken in a site adjacent to our study area by Osem et al. (2006). In total, we gathered trait data for the following numbers of annual plant species: SLA – 134 species, CH and SRH – 137 species, SM – 115 species, SN – 110 species. A complete list of species, their functional trait values and their occupancies in the three land units is provided in the supplementary material (Table A3).

Based on the species survey data, we calculated that our trait data set accounts for 60–75% of annual species and for 80–95% of annual plant individuals in the 15 m × 15 m plots and therefore provides a reliable representation of community-level trait indices (Pakeman and Quested, 2007).

Data analysis and statistics

Prior to the calculation and analysis of community-level trait indices, we assessed the univariate distribution and bivariate correlations of species' mean trait values. Species' mean trait values for CH, SRH, SN and SM showed a right-skewed distribution. Therefore, we used a $\log_{10}$-transformation to normalize these traits (Westoby, 1998; Fonseca et al., 2000). Species' SLA values were normally distributed. We analysed pair-wise correlation between species-level traits by non-parametric Spearman rank correlation of untransformed trait data.

Null-model tests for community assembly processes

In order to test for convergence and divergence in trait values, we calculated several community-level trait indices for each sampling plot and contrasted these values with indices derived from null-models based on random community assembly.

Trait convergence was assessed by measuring the range and variance of trait values in a community, both of which are expected to be reduced by habitat filtering. We combine these indices, as each of them has its advantages and shortcomings. Trait range closely represents the concept of habitat filtering and is independent of trait divergence within communities, but it is sensitive to extreme trait values. In contrast, trait variance is simultaneously determined by convergence due to filtering and divergence due to competition, but it is more robust to extreme trait values (Cornwell and Ackerly, 2009).

Interspecific competition is expected to result in a limiting similarity and/or an even spacing among species trait values and thus in a platykurtic distribution of trait values in communities (Stubbs and Wilson, 2004; Kraft and Ackerly, 2010; Götzenberger et al., 2012). Accordingly, we used the kurtosis of the community-level trait distribution as well as three indices based on distances along trait axes to test for trait divergence. First, we used the standard deviation of nearest neighbour distances (sdNN), which directly mirrors the idea of limiting similarity, and second we calculated the standard deviation of the consecutive neighbour distances (sdND) of species trait values ordered along the respective trait axis, which quantifies the evenness of trait spacing (Cornwell and Ackerly, 2009; Kraft and Ackerly, 2010). In order to control for habitat filtering while testing for trait divergence, we followed the recommendation by Kraft and Ackerly (2010) and used range-standardized indices sdNNr and sdNDr, which were obtained by dividing sdNN and sdND by the observed trait range in the community. As the neighbour distances sum up to the trait range and are thus, by definition, related to the trait range of a plot, we only used the range-standardized version of this index (sdNDr).

We implemented three different null-models that reflect different levels of randomness in community assembly and account for habitat filtering in different ways. All three null-models maintained the observed species richness of sampling plots and the probability of assembling a species into a null-community was proportional to its plot-level incidence in the survey data (Gotelli and Graves, 1996; Kraft et al., 2008; Kraft and Ackerly, 2010). In null-model 1, we used the same regional species pool for all plots, irrespective of their position along the S–N gradient, thus testing for habitat filtering in sampling plots relative to the regional species pool. In null-model 2 species occurrences were only randomized within land units by using specific species pools for each land unit. In this way, null-model 2 was used to test for habitat filtering in sampling plots relative to land unit specific species pools.

In null-model 3 we adopted the two-step approach of Cornwell and Ackerly (2009). For each 15 m × 15 m plot sampling plot we first derived a specific species pool, which includes only those species with trait values that are within the observed trait range of this sampling plot. Then, null communities for this plot were randomly assembled from this plot-specific species pool only. This null-model strictly controls for trait convergence at the sampling plot scale and is therefore only used for tests of trait divergence.

We calculated trait indices and tested for community assembly processes at four different scales: 15 m × 15 m, 5 m × 5 m, 1 m × 1 m, and 0.25 m × 0.25 m. In null-model 3, we used the trait range observed at the 15 m × 15 m scale to derive plot-specific species pools for the scales of 5 m × 5 m, 1 m × 1 m, and 0.25 m × 0.25 m. Accordingly, null-model 3 assumes that habitat filtering due to climate, patch area and/or isolation mainly operates at scales larger than the plot size of 15 m × 15 m, while non-random trait distributions at smaller scales (5 m × 5 m, 1 m × 1 m and 0.25 m × 0.25 m) are assumed to be primarily driven by interspecific competition (Cornwell and Ackerly, 2009).

At the smallest scale of 0.25 m × 0.25 m observed species richness is often low, especially in Dvir due to a low plant density (Giladi

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et al., 2011). With very low species number, community-level trait indices cannot be reliably estimated and therefore we excluded all 0.25 m × 0.25 m plots with less than five species. This threshold lead to an exclusion of 31% of all plots, with much higher exclusion rate in Dvir (64%) compared to Lachish (13%) and Galon (17%). Due to the high total number of small sampling plots the tests for trait divergence and convergence are still feasible after the exclusion of low diversity plots, but the imbalance in sampling size between land units should be kept in mind when interpreting the results.

For each null model and each scale, we simulated 1999 random permutations to generate expected trait indices (T_{exp}) under random assembly. We used the mean trait index of all 1999 permutations as expected value under the null model. We tested the deviation of observed values vs. null expectations using paired Wilcoxon signed rank tests (Kraft et al., 2008). All tests were one-tailed with the expectation of lower trait ranges and variances due to habitat filtering and lower kurtosis and standard deviations of nearest neighbour and neighbour distances due to competition. Standard effect sizes (SES) for each plot and each trait index (T) were calculated as:

$$\mathrm{SES} = \frac{T_{\mathrm{obs}} - \bar{T}_{\mathrm{exp}}}{\mathrm{sd}(T_{\mathrm{exp}})},$$

where T_{obs} is the observed trait index and T_{exp} the expected trait index. The standard deviation in the denominator of T_{exp} was calculated from the 1999 null-model simulations (Kraft et al., 2008; Cornwell and Ackerly, 2009; Kraft and Ackerly, 2010).

Subsequently, we assessed if the strength of trait convergence and divergence varied along the S–N gradient, with patch area or patch connectivity. For this purpose we tested whether the standard effect sizes (SES) differ significantly between land units, using rank-based Kruskal–Wallis-tests, and if the SES correlate with patch area or connectivity, using Spearman rank correlation tests. According to the expectation that habitat filtering due to climate and fragmentation operates at large scale, while annual plants compete at small scales (Kraft and Ackerly, 2010), we restricted these tests to the largest spatial scale (15 m × 15 m) in the case of trait convergence indices and to the smallest spatial scale (0.25 m × 0.25 m) in the case of trait divergence indices. With SES values derived from null-model 1, we tested only differences between land units, while with SES values derived from null-model 2, we tested correlations with patch area and connectivity. This reflects the expectations that null-model 1 tests primarily for habitat filtering between land-units due to the S–N gradient, while null-model 2 tests primarily for habitat filtering within land-units due to differences in patch area or connectivity.

Shifts of plant strategies along the south–north gradient and with fragmentation

After testing the effects of habitat filtering and competition on community trait distributions, we assessed the effects of fragmentation and position along the S–N gradient on community-level traits. For this purpose we calculated community-mean trait values by averaging trait values of all annual species present at the 15 m × 15 m plot scale using equal weights for all species (Cornwell and Ackerly, 2009; Golodets et al., 2009).

The position along the S–N gradient was used as a categorical factor, called land unit, with the three levels Dvir, Lachish and Galon. Habitat fragmentation was represented by patch area ($\log_{10}$-transformed) and by patch connectivity, as described above. We analysed collinearity between explanatory variables using robust Spearman-correlation analysis for testing patch area vs. patch connectivity and Kruskal–Wallis tests for testing land unit vs. both continuous patch variables.

Due to the nested structure of our sampling design with 1–3 plots in one patch, we used linear-mixed effects models (lme) with patch ID as a random factor and with land unit, $\log_{10}$(patch area) and patch connectivity as fixed-effect explanatory variables (Pinheiro and Bates, 2000). In addition, we included all three two-way interactions (land unit × $\log_{10}$(patch area), land unit × connectivity, $\log_{10}$(patch area) × connectivity). The inclusion and exclusion of the three main effects and the interaction terms lead to 18 possible models for each community-mean trait value. We calculated the $\mathrm{AIC_c}$ (AIC for small sampling sizes) for each of these models and used the $\mathrm{AIC_c}$ values for model selection and to assess the importance of the explanatory variables on community-mean trait values (Burnham and Anderson, 2001; Burnham et al., 2011). First, we selected the best model with the lowest $\mathrm{AIC_c}$ and all models whose difference in $\mathrm{AIC_c}$ with the best model was less than two units. In addition, we calculated the Akaike weights for all the *a priori* chosen 18 models and, for each explanatory variable we used the sum of these weights as a measure of the relative importance of this variable (Burnham and Anderson, 2001).

Finally, we checked whether our models might be biased by spatial autocorrelation. For this purpose, we first tested the model residuals for differences of among land units using Kruskal–Wallis tests and second, we calculated correlograms of the model residuals based on Moran's I for each land unit (Dormann et al., 2007). Model fitting and analysis was carried out using R (R Core Team, 2012) and the packages `nlme`, `AICmodavg`and `ncf`.

Results

Correlations among explanatory variables and species' trait values

In our study landscape field capacity as well as soil organic matter content increased along with precipitation from south to north (Table 2, supplementary material Fig. A2). In contrast, neither patch area nor connectivity was correlated with any soil variable or with the position along the S–N gradient (supplementary material Figs. A2 and A3)

Interspecific trait correlations, which reflect morphological associations between certain trait attributes, were explored prior to any analysis of community-level trait indices (Table 3). Seed release height and canopy height were strongly and positively correlated. Seed mass and seed number were negatively correlated, reflecting a seed size–seed number trade-off among annual plant species. A relatively weak, but significant positive correlation was found between each of the height measurements (CH and SRH) and seed mass. Interestingly, SLA was not correlated with any other trait.

Significant correlations among traits at the species level imply that the potential response of these traits to habitat filtering and competition cannot be considered statistically independent. Therefore, we only used one of the closely correlated plant height measurements (canopy height) for any further analyses at the community level. Seed mass and seed number were analysed independently, but we consider the seed size–seed number trade-off

Table 3
Spearman rank correlation coefficients (ρ) for species trait values. Correlations were calculated with untransformed species trait values using species ranks. Significant correlations ($p < 0.05$) are shown in bold. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SRH – seed release height; SM – seed mass; SN – seed number.

	SLA	CH	SRH	SM
CH	0.11			
SRH	0.12	**0.90**		
SM	−0.15	**0.42**	**0.36**	
SN	0.07	0.15	0.17	**−0.55**

Table 4
Wilcoxon signed rank tests of community assembly processes at the landscape level. Three different null-models were used to account for trait convergence due to habitat filtering at different scales. (a) Null-model 1 did not consider trait convergence. (b) Null-model 2 controls for trait convergence within land units and (c) null-model 3 for trait convergence at the sampling plot scale. In null-model 3 trait ranges observed at the 15 m × 15 m scale were used to restrict simulated trait ranges at the 0.25 m × 0.25 m sampling scale. *p*-Values are reported for the one-tailed and paired test of the hypothesis that the observed trait index is lower than under the null-model. Significant deviations from the null-model ($p < 0.05$) are shown in bold. Abbreviations of trait divergence indices: sdNN – standard deviation of nearest-neighbour distance; sdNNr – sdNN divided by trait range; sdNDr – standard deviation of ordered neighbour distances divided by trait range. See the main text for the definitions of trait indices and the implementation of the null models. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number.

Trait and scale	Trait convergence		Trait divergence			
	Range	Variance	Kurtosis	sdNN	sdNNr	sdNDr
(a) Null-model 1 – regional species pool						
SLA						
15 m	**0.008**	0.529	**0.050**	**<0.001**	**<0.001**	**<0.001**
0.25 m	**0.016**	**<0.001**	0.166	**0.003**	0.466	0.634
CH						
15 m	**0.011**	**0.001**	**0.035**	**0.001**	**0.004**	**<0.001**
0.25 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SM						
15 m	**0.003**	**0.004**	**0.035**	**<0.001**	**0.001**	**<0.001**
0.25 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SN						
15 m	0.109	0.077	0.074	**0.007**	**0.041**	**0.017**
0.25 m	**0.047**	**0.015**	**<0.001**	**<0.001**	**<0.001**	0.077
(b) Null-model 2 – land unit specific species pool						
SLA						
15 m	0.054	0.461	0.286	**<0.001**	**<0.001**	**0.024**
0.25 m	**0.009**	**<0.001**	0.273	**0.007**	0.637	0.922
CH						
15 m	**0.009**	**0.001**	0.190	**<0.001**	**0.002**	**0.013**
0.25 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SM						
15 m	**0.007**	**0.009**	**0.024**	**0.002**	**0.009**	**<0.001**
0.25 m	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
SN						
15 m	**0.036**	0.157	0.123	**0.003**	**0.015**	**0.009**
0.25 m	**0.031**	**0.008**	**<0.001**	**<0.001**	**<0.001**	0.115
(c) Null-model 3 – plot specific species pool						
SLA						
15 m			0.870	0.887	0.244	0.076
0.25 m			0.289	0.149	0.622	0.519
CH						
15 m			1.000	0.817	0.198	0.450
0.25 m			**<0.001**	**0.001**	**0.008**	**0.001**
SM						
15 m			1.000	1.000	1.000	1.000
0.25 m			**0.001**	0.198	**0.011**	**<0.001**
SN						
15 m			0.996	1.000	0.934	0.669
0.25 m			**0.007**	0.277	**0.002**	**0.048**

Table 5
Spearman rank correlation coefficients (ρ) between standard effect sizes (SES), patch area and connectivity. SES values were derived for trait convergence indices with null-model 2 at the scale of 15 m × 15 m. Significant correlations ($p < 0.05$) are shown in bold. See the main text for the definitions of trait indices and the implementation of the null model. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number.

Trait	Area		Connectivity	
	Range	Variance	Range	Variance
SLA	**0.36**	**0.36**	**0.28**	**0.27**
CH	−0.16	−0.17	0.06	0.09
SM	**−0.47**	**−0.41**	0.00	0.06
SN	0.16	0.10	−0.12	−0.17

and the association between plant height and seed mass while discussing our results.

Community assembly at different hierarchical scales

We tested for non-random patterns in functional trait distributions using three null-models, four traits, four sampling scales and six community-level trait indices, two of which reflect trait convergence (trait range and variance) and four reflect trait divergence (trait kurtosis, sdNN, sdNNr, sdNDr). Here, we present results for the largest (15 m × 15 m) and smallest (0.25 m × 0.25 m) sampling scales only (Table 4), since the tests at the 5 m × 5 m and 1 m × 1 m sampling scales provided intermediate results. Test results and standard effect sizes for all sampling scales are presented in the supplementary material (Tables A1 and A2).

When we tested for habitat filtering in sampling plots relative to the regional species pool (null-model 1), we found a significant reduction of trait ranges and variances for canopy height and seed mass at both sampling scales. For SLA the evidence varied with trait index and sampling scale, with significantly lower trait ranges at the large scale and significantly lower trait ranges and variances at the small scale. For seed number we only found a significant reduction of trait ranges and variances at the small scale (Table 4a). The comparison of standard effect sizes (SES) between land units at the large scale revealed that SES of SLA did not differ between land units, but SES of all other traits were lower in Galon. Since lower, i.e. more negative, SES indicate stronger effects, this implies a more intense habitat filtering of all traits except SLA in the mesic sites (Fig. 2).

Using null-model 2, which tests for habitat filtering in sampling plots relative to land unit specific species pools, there was again strong evidence for trait convergence of canopy height and seed mass, irrespective of trait index and sampling scale. For SLA there was only a significant reduction of trait ranges and variances at the small scale. For seed number we found a significant reduction of trait ranges at the large scale, but for both convergence indices at the small scale (Table 4b).

Despite the insignificant trait convergence of SLA at the large scale, the corresponding standard effect sizes were positively correlated with patch area and connectivity. For the SES of seed mass ranges and variances we found a negative correlation with patch area, which indicates stronger habitat filtering for seed mass in larger patches (Table 5).

With respect to trait divergence, the evidence for limiting similarity and even spacing of species trait values also varied among traits, scales and trait indices, but we found the most striking result considering the different null-models. When we did not restrict the trait range of simulated communities (null-models 1 and 2) our results indicate evidence for trait divergence for all four traits and at all sampling scales (Table 4a and b). However, when the trait ranges of simulated communities were restricted to the observed trait ranges at the 15 m × 15 m scale (null-model 3) all significant effects disappeared at the large scale. At the small scale there was still significant evidence for trait divergence of canopy height, seed mass and seed number (Table 4c).

The comparison of trait divergence effect sizes between land units indicated some significant differences, especially more negative SES, i.e. stronger divergence, of seed number in Dvir (Fig. 3). For seed mass we also found significant correlations of divergence indices with patch area and connectivity (Table 6). Despite significant effects, the differences in median SES between land units (Fig. 3) as well as the correlation coefficients (Table 6) were comparably low. Due to the low species number in Dvir, the imbalance in the data set after the exclusion of very low diversity plots, and

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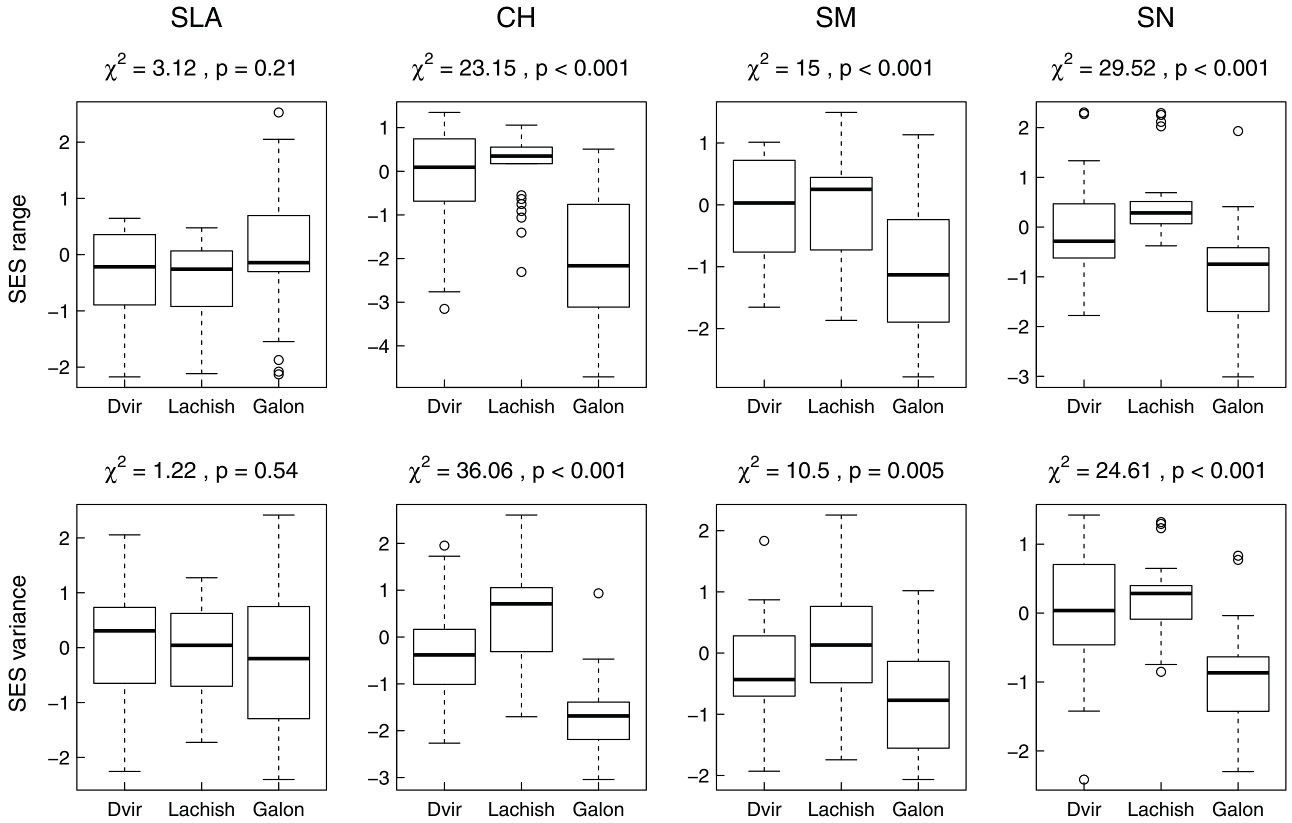

Fig. 2. Standard effect sizes (SES) for trait convergence indices in different land units (Dvir, Galon, and Lachish – from south to north). SES values were derived with null-model 1 at the scale of 15 m × 15 m. Kruskal–Wallis tests were applied to test for significant differences between land units. See the main text for the definitions of trait indices and the implementation of the null model. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number.

Table 6
Spearman rank correlation coefficients (ρ) between standard effect sizes (SES), patch area and connectivity. SES values were derived for trait divergence indices with null-model 3 at the scale of 0.25 m × 0.25 m. Significant correlations ($p < 0.05$) are shown in bold. See the main text for the definitions of trait indices and the implementation of the null model. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number.

Trait	Area				Connectivity			
	Kurt	sdNN	sdNNr	sdNDr	Kurt	sdNN	sdNNr	sdNDr
SLA	0.01	0.02	0.00	0.07	−0.06	−0.01	−0.02	−0.03
CH	0.04	0.02	0.05	0.04	0.00	0.01	0.02	−0.03
SM	0.01	0.02	0.02	0.08	0.03	0.01	0.00	0.06
SN	**−0.11**	−0.03	−0.08	0.00	**0.15**	**0.11**	**0.17**	0.03

Table 7
Linear mixed-effects models (lme's) of community mean traits values. For each model the following information is provided: the number of parameters (K), the AIC value for low sample size (AIC_c), the difference in AIC_c to the best model (ΔAIC_c) and the Akaike weights (AIC_cwt). Only models with $\Delta AIC_c < 2$ are shown. Community mean traits were derived as equally-weighted average of species traits at 15 m × 15 m sampling plots. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number. Abbreviations of explanatory variables: LU – land unit; Area – $\log_{10}$(patch area); Con – patch connectivity.

Model	K	AIC_c	ΔAIC_c	AIC_cwt
SLA ∼ LU + Area	6	122.07	0	0.34
SLA ∼ LU + Area + LU × Area	8	122.44	0.36	0.29
CH ∼ LU + Area + Con	7	−222.47	0	0.30
CH ∼ LU + Area + Con + LU × Con	9	−221.12	1.35	0.16
SM ∼ LU + Area + Con + LU × Area + LU × Con	11	−114.73	0	0.23
SM ∼ LU + Area + Con + LU × Area + LU × Con + Area × Con	12	−114.34	0.39	0.19
SM ∼ LU + Area + Con + LU × Area	9	−113.26	1.47	0.11
SN ∼ LU + Area + LU × Area	8	−137.65	0	0.28
SN ∼ LU + Area + Con + Area × Con	8	−136.36	1.29	0.15
SN ∼ LU + Area	6	−136.28	1.37	0.14
SN ∼ LU + Area + Con + LU × Area + Area × Con	10	−135.92	1.73	0.12

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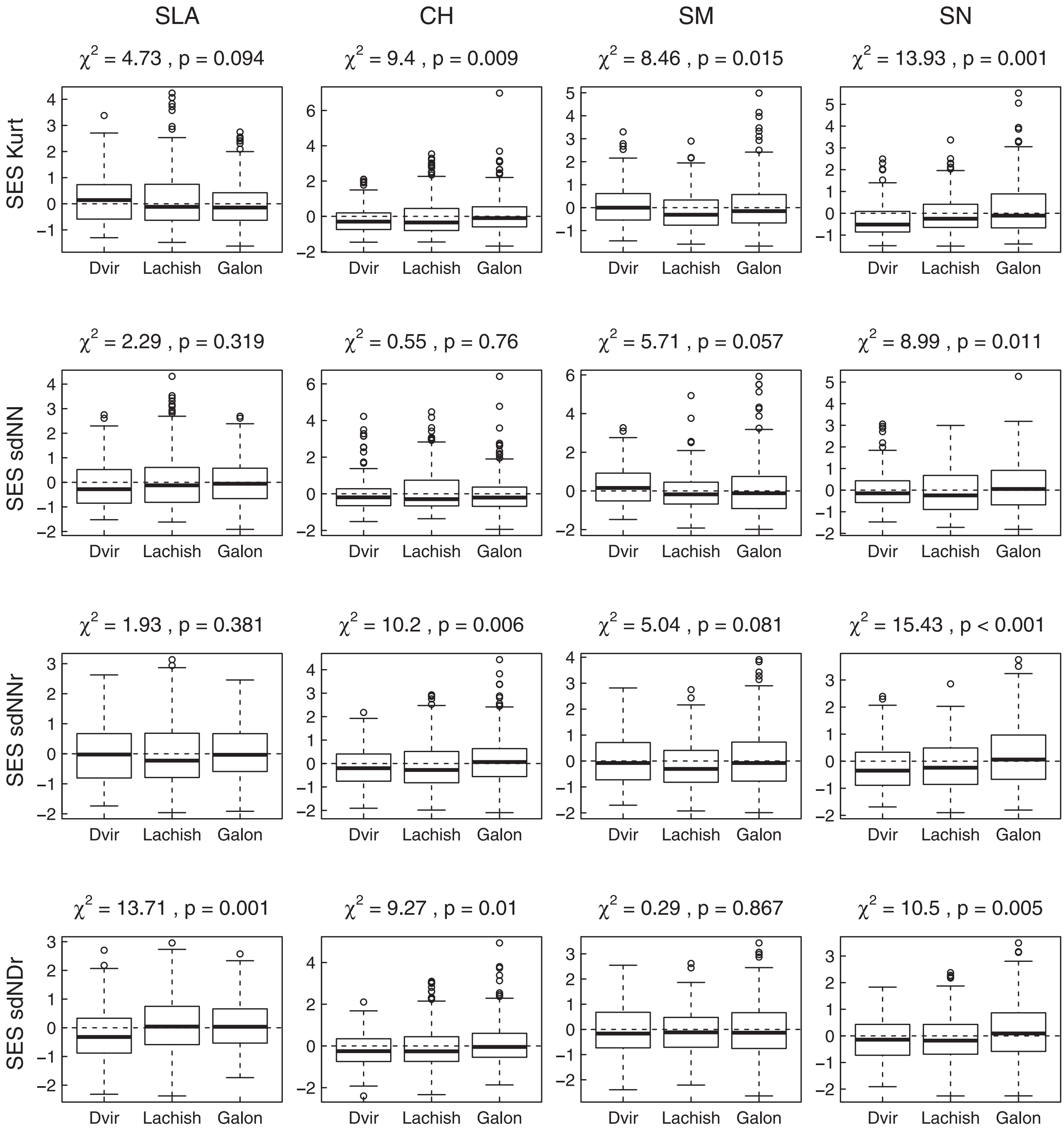

Fig. 3. Standard effect sizes (SES) for trait divergence indices in different land units (Dvir, Galon, and Lachish – from south to north). SES values were derived with null-model 3 at the scale of 0.25 m × 0.25 m. Kruskal–Wallis tests were applied to test for significant differences between land units. See the main text for the definitions of trait indices and the implementation of the null model. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number.

the statistical issue that with high sample size even minor effects indicate significance, the observed associations of SES at the small scale to land unit, patch area and connectivity should be interpreted with caution.

Shifts in community-mean trait values along the S–N gradient and with habitat fragmentation

The linear mixed-effects models revealed significant shifts of community-mean trait values with the S–N gradient and with habitat fragmentation (Table 7). Community-mean values of all traits were significantly associated with land unit and with patch area, while community means of canopy height and seed mass were additionally driven by patch connectivity. Especially for community-mean seed mass and seed number there is evidence for varying response to patch area and/or connectivity along the S–N gradient (Tables 7 and 8; Fig. 5). In the following we will only describe the effects of model terms with Akaike weights of at least 0.5 in order to focus on the associations with high statistical significance (Table 8). To improve readability, we will use simple trait names, but always refer to community-mean trait values.

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Table 8
Sum of Akaike weights for all models that include a certain explanatory variables. The sum for each community-mean trait was derived from all 18 possible models. Trait abbreviations: SLA – specific leaf area; CH – canopy height; SM – seed mass; SN – seed number. Abbreviations of explanatory variables: LU – land unit; Area – $\log_{10}$(patch area); Con – patch connectivity.

Trait	Model term					
	LU	Area	Con	LU × Area	LU × Con	Area × Con
SLA	1.00	0.95	0.33	0.45	0.04	0.08
CH	1.00	0.87	0.83	0.18	0.28	0.16
SM	1.00	0.91	0.84	0.66	0.57	0.35
SN	1.00	0.97	0.56	0.55	0.16	0.39

SLA increased from south to north (Fig. 4a) and was negatively associated with patch area (Fig. 5b). Canopy height was higher in Galon, compared to Lachish and Dvir (Fig. 4b) and was negatively associated with patch connectivity and patch area (Fig. 5b). For SLA and canopy height there was little evidence for shifts in trait associations with fragmentation indices along the S–N gradient, indicated by low Akaike weights of the interaction terms (Table 8).

Seed mass increased from south to north when only the main effect of land unit was considered (Fig. 4c). The association of seed mass with fragmentation significantly varied along the S–N gradient (Tables 7 and 8). Seed mass was negatively associated with patch connectivity and positively associated with patch area in the northernmost land unit – Galon – but we found no associations of seed mass with any fragmentation variable neither in Lachish nor in Dvir (Fig. 5e and f).

Seed number tended to decrease along the S–N gradient (Fig. 4d). Seed number was not affected by patch connectivity (Fig. 5g), but the association with patch area varied along the S–N gradient from a clear negative association in the north (Galon), to a weakly negative association in Lachish and no association at all in Dvir (Fig. 5h).

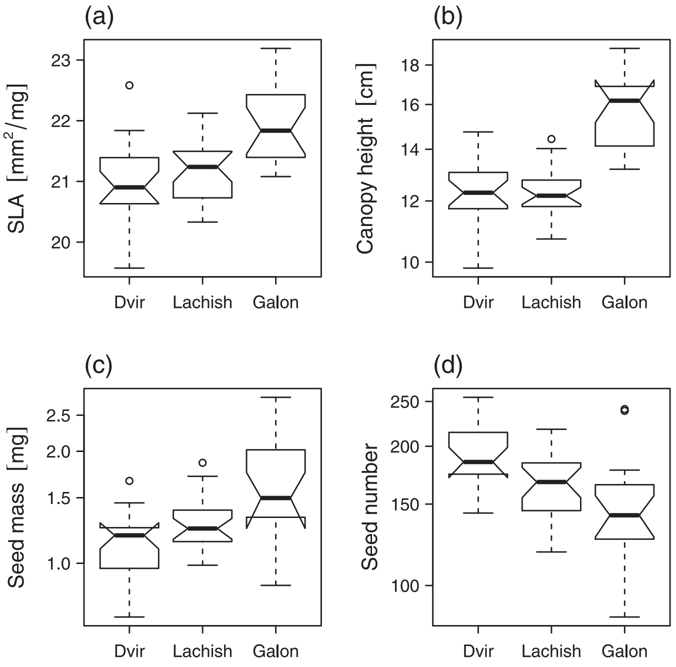

Fig. 4. Distribution of community-mean traits along the S–N gradient, represented by the land units – Dvir, Lachish and Galon (from south to north). Species traits were averaged at 15 m × 15 m sampling plots. Boxes indicate median and quartiles (25% and 75% quantiles), and whiskers indicate minimum and maximum (if there are no outliers). Values, which are more extreme than the quartiles ± 1.5 × IQR (interquartile distance), are classified as outliers and shown as dots. The notches provide robust 95% confidence for the medians. If two notches do not overlap there is strong evidence that the two medians differ significantly.

We tested if our model results might be flawed by spatial autocorrelation. However there was no systematic variation of model residuals among land units and no indication of spatial autocorrelation within the land units (supplementary material, Figs. A4 and A5).

Discussion

Evidence for community assembly processes

Our findings indicate that habitat filtering causes trait convergence within local communities compared to the regional species pool (null-model 1) for all functional traits studied here. While habitat filtering of SLA did not differ along the S–N gradient, the filtering of canopy height, seed mass and seed number might be stronger in mesic sites (Fig. 2). When local communities were compared to land unit specific species pools, there was still strong evidence for trait convergence especially of plant height and seed mass (null-model 2). In both null-models trait convergence was evident across all spatial scales studied here.

In contrast, the evidence for trait divergence due to interspecific competition fundamentally depended on the specific null-model and the sampling scale. Due to the strong evidence for habitat filtering, we presume that controlling for trait convergence while testing for trait divergence is most appropriate in our study area (null-model 3). However, when we accounted for habitat filtering effects in the null-model, we only found evidence for trait divergence at the smallest sampling scale. Considering the small size of annual plant species, it is plausible that the smallest scale studied here (0.25 m × 0.25 m) best represents the scale at which annual plants actually compete for resources. Similar to our finding, Kraft and Ackerly (2010) found the strongest evidence for trait divergence of co-occurring tree species at the scale of 5 m × 5 m, which was the smallest scale they investigated in a tropical rain forest and a plausible scale for competitive interactions among trees.

The Southern Judean Lowlands are characterized by a sharp productivity gradient that corresponds with substantial increases in precipitation, soil fertility (indicated by soil field capacity and organic matter content), plant density (Giladi et al., 2011) and vegetation biomass (Schmidt and Gitelson, 2000) from south to north. As these productivity related gradients are observed in an area with similar geology and temperatures (Table 2; Kloner and Tepper, 1987; Goldreich, 2003), we presume that precipitation is the main underlying driver of the trends in the other variables (Holzapfel et al., 2006; Harel et al., 2011). Accordingly, we interpret the trait convergence in communities relative to the regional species pool as primarily reflecting trait adaptation to this productivity gradient (Cornwell and Ackerly, 2009; Harel et al., 2011). In contrast, the trait convergence in local communities relative to the species pool of a specific land unit might be related to differences in patch area and connectivity or other unmeasured patch-level characteristics (Lindborg et al., 2012; Marini et al., 2012).

Habitat filtering and interspecific competition are expected to drive trait distributions simultaneously. Therefore, testing for competition effects requires controlling for habitat filtering effects (Ackerly and Cornwell, 2007; Cornwell and Ackerly, 2009). For this purpose Kraft and Ackerly (2010) suggested using trait divergence indices, which are standardized by trait ranges (sdNNr, sdNDr). When we applied these indices, we found strong evidence for trait divergence across all traits and sampling scales (null-models 1 and

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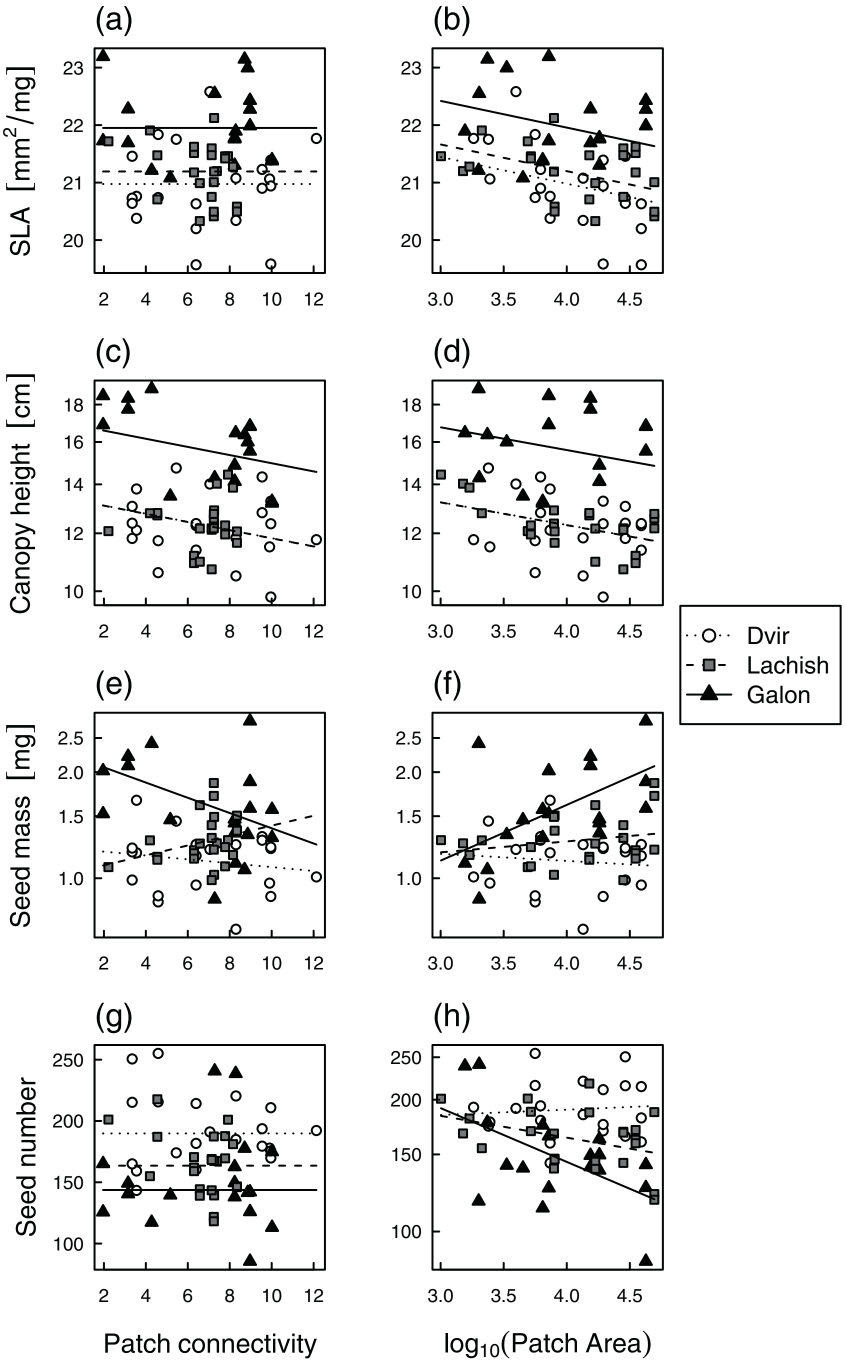

Fig. 5. Association of community-mean trait values with patch connectivity (left column) and patch area (right column). The regression lines show predictions of mixed-effects models for each land unit (compare Table 5). The patch variable (area or connectivity) which is not shown in the respective panel was fixed at its mean value averaged over all patches. Within the panels, regression lines with different slopes indicate a significant interactive effect of land unit and the respective fragmentation index (patch area or connectivity).

2). However, when we used the two-step procedure of Cornwell and Ackerly (2009), where the species pool for each local community was restricted by the observed trait range of this community, the evidence for trait divergence was restricted to the smallest sampling scale (null-model 3). This finding underlines the importance and emphasizes the challenge of choosing an appropriate sampling scale, null-model and specifying an appropriate species pool for the question under study (De Bello, 2012; De Bello et al., 2012).

Our findings of convergence across all scales, but of divergence only at the smallest scale, seem to indicate that habitat filtering is more important for community assembly in the SJL than interspecific competition. However, this argumentation does not consider two important points: First, the evidence for trait convergence and divergence is conditioned on the set of traits chosen to be included in an analysis. It is possible that competition affects functional traits that were not measured and that might indeed be very difficult to measure (Silvertown, 2004; Götzenberger et al., 2012). In particular, root traits that are related to water acquisition might be of high interest and relevance for competition among plant species in arid regions such as our study area.

Second, the expectation of trait divergence as an outcome of interspecific competition might be too simplistic: Classical niche theory predicts that competitive exclusion of species with similar traits and high niche-overlap results in a "limiting similarity" among co-occurring species or an even spacing of their trait values (MacArthur and Levins, 1967; Stubbs and Wilson, 2004; Kraft et al., 2008). A more recent perspective on competition and traits challenges this prediction (Grime, 2006; Mayfield and Levine, 2010; De Bello et al., 2012; Spasojevic and Suding, 2012). In general, coexistence is determined by the relative fitness differences and the niche differentiation among competing species (Chesson, 2000). Stable coexistence is only possible with substantial niche differentiation, but even without any stabilizing niche differentiation species can coexist over ecologically relevant timescales, as long as they are equivalent in fitness and competitive ability (Chesson, 2000; Hubbell, 2001). Mayfield and Levine (2010) argued that trait differences among species trait can also translate into large fitness differences rather than into stabilizing niche differentiation. Under these circumstances species with high trait dissimilarity will be preferentially excluded and thus competition result in trait convergence instead of trait divergence (De Bello et al., 2012).

For instance, in productive environments all species need to be adapted to high plant density and high competitive pressure. Accordingly, trait adaptation to productive environments has been also called a "productivity filter" (Grime, 2006). This terminology can be confusing as the "productivity filter" essentially refers to consequences of competitive pressure, but it indicates that especially in productive habitats competition might also drive trait convergence analogously to abiotic habitat filtering in the strict sense.

Functional trait associations with the south–north gradient

The positive association of SLA with the position along the S–N productivity gradient found in our study closely corresponds to findings of previous studies of leaf morphology along precipitation and productivity gradients ranging from landscape to global scales (Fig. 4a; Fonseca et al., 2000; Ackerly et al., 2002; Wright et al., 2004). Low SLA is associated with thick and/or dense leaves and is known to reflect leaf adaptations to low water availability, high evapotranspiration and/or resource stress, while high SLA mirrors species adaptations to higher growth rates and higher competitive pressure within more productive communities (Reich et al., 1999; Westoby et al., 2002). Similarly, our finding of taller plant communities in the northern, mesic patches can be viewed as an adaptation for intensified competition for light in a more productive and competitive ecosystem (Fig. 4b; Grime, 2001; Westoby et al., 2002).

The increase in plant density and productivity along the S–N gradient also provides an explanation for the observed increase in community-level seed mass (Fig. 4c). High seed mass conveys a competitive advantage for seedlings, an advantage that might be most important in mesic and competitive environments (Leishman et al., 2000; Moles and Westoby, 2004; Metz et al., 2010; Harel et al., 2011). However, as seed mass and plant height are weakly, but positively correlated at the species level, the increase in seed mass might be, at least partly, driven by selection for greater plant height. Overall the increase of community-mean SLA, plant height and seed mass along the S–N reflects increasing species adaptation to productivity and competitive pressure, or – using the terminology of Grime (2006) – an increasing importance of the "productivity filter". This conclusion is further supported by our observation of stronger trait convergence effects of plant height and seed mass at the northern, mesic end of the gradient (Fig. 2).

Our analysis provides evidence for a seed size–seed number trade-off among annual plant species (reviewed in Leishman et al., 2000), which implies that the response of community-level seed number is associated with the response of community-level seed mass. Therefore, the decrease in seed number along the S–N gradient may actually follow the selection for an increasing seed mass along that gradient (Fig. 4d). However, the increase in seed number with increasing aridity might also reflect an adaptation to the harsh and unpredictable conditions in arid environments, which select for high reproductive allocation as well as for bet-hedging strategies (Venable and Brown, 1988; Aronson et al., 1990; Petrů et al., 2006; Siewert and Tielbörger, 2010). Venable and Brown (1988) suggested large seed size, dispersal and dormancy as three potential bet-hedging strategies. Considering the low community-level seed mass we found in the arid sites, we speculate that plant communities there do not rely on large seed size as a bet-hedging strategy, but rather on dispersal and/or dormancy. However, while seed dormancy has been suggested as an important bet-hedging strategy in arid and semi-arid environments (Venable, 2007; Petrů and Tielbörger, 2008; Siewert and Tielbörger, 2010), there is evidence that at least germination under optimal conditions is higher in arid than in Mediterranean environments (Harel et al., 2011). This mismatch between theoretical predictions and empirical evidence indicates the need for further research on the relationship between morphological seed traits and bet-hedging strategies of plant species.

In addition to habitat productivity, livestock grazing might be an important driver of plant functional traits in our study area. Along the S–N gradient studied here, there is a shift from sheep and goat grazing in the southern, arid sites to cattle grazing in the northern, mesic sites (Rotem, 2012). Grazing intensity is known to be negatively associated with community-level plant height (Osem et al., 2004; Díaz et al., 2007; Golodets et al., 2009). Accordingly, our finding of increasing plant height from south to north may reflect a decrease of grazing pressure in addition to the increase in productivity. Furthermore, the increase in SLA might indicate a shift from grazing avoidance by mechanical or chemical defences, which is associated with low SLA, to grazing tolerance by high regrowth capacity after defoliation by herbivores, associated with high SLA (Bullock et al., 2001). Especially in landscapes with long grazing history plant functional traits are known to reflect convergent selection for grazing resistance and the specific environmental conditions in the landscape (Milchunas et al., 1988; Osem et al., 2004; De Bello et al., 2005). Therefore, we hypothesize that the community-level plant functional traits in our southern, arid sites mirror convergent adaptation to grazing and drought-stress. Separating grazing and habitat fragmentation effects on plant functional traits by long-term grazing exclusion plots along the S–N gradient could provide an interesting follow up to the study presented here.

Functional trait associations with fragmentation along the S–N gradient

We predicted that isolated patches and, due to the rescue-effect also small patches, favour species with high colonization ability (Brown and Kodric-Brown, 1977; Hanski, 1999). In addition, small patches are expected to include a disproportionally high percentage of species with long persistence times (Lindborg et al., 2012). Furthermore, we hypothesized that trait attributes that convey high persistence vary along the S–N gradient, which represents a shift from a stress-dominated system (arid) to a competition-dominated system (mesic). Therefore, we predicted that small

Please cite this article in press as: May, F., et al., Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. Perspect. Plant Ecol. Evol. Syst. (2013), http://dx.doi.org/10.1016/j.ppees.2013.08.002

patches will host communities with higher drought-adaptation (lower SLA, smaller seeds) in the arid sites and higher competitive ability (taller plants, higher SLA, larger seeds) in the mesic sites (compare Table 1).

We found that SLA was negatively associated with patch area, but this association did not significantly vary among the land units (Fig. 5b). This finding corresponds to our prediction for the mesic sites, but contrasts our expectation for the arid sites, which might indicate that fast growth is important for species persistence in small patches along the entire S–N gradient. Our predictions regarding negative associations between community-level plant height and patch connectivity, as well as between plant height and patch area, were both supported (Fig. 5c and d). Isolated and small patches might favour taller species, as these species release their seeds at greater height and therefore may achieve longer dispersal distances leading to higher colonization rates (Tackenberg et al., 2003; Thomson et al., 2011). Alternatively, the negative associations between plant height and fragmentation indices (patch area and connectivity) could also be explained by an association of grazing with fragmentation, for instance if small and isolated patches are less attractive for pastoralist. However, in a study that was conducted in the same landscape, which used counts of livestock faeces as a measure of grazing intensity, there was no evidence for such an association (Rotem, 2012).

In contrast to plant height, the response of seed mass to patch connectivity changed along the S–N gradient, but in a different way than expected. Considering the higher colonization ability of species producing many seeds, we predicted decreasing seed number and – due to the seed size–seed number trade-off – increasing seed mass with increasing patch connectivity. However, we found the contrasting pattern of a negative association between seed mass and patch connectivity in the mesic sites and no association in the more arid sites (Fig. 5e). We suggest that the pattern observed in the mesic sites might emerge from a closer association of seed mass to seedling survival (Metz et al., 2010) than to colonization ability (Thomson et al., 2011). As explained above, in the mesic environment, seedling competition may be intense and the competitive advantage conveyed by larger seeds may result in the exclusion of species with smaller seeds from isolated patches (Moles and Westoby, 2004). If immigration rates are low in these isolated patches, the process of exclusion of competitively inferior species might be faster than the immigration of good colonizers (Eriksson, 1996; Lindborg, 2007; Johansson et al., 2011). Moving south, this relationship disappears as seedling competition and thus the competitive advantage of large seedlings become less important with lower productivity and lower plant density (Harel et al., 2011).

The association of seed mass to patch area showed the inverse pattern of the seed number response and might therefore be driven by the association of seed number with patch area – as discussed in the following – and the seed size–seed number trade-off. Our prediction of a negative association between seed number and patch area was confirmed, but this association was limited to the mesic sites (Fig. 5h). Species with high seed number are expected to be better colonizers due to the higher probability that at least some seeds are dispersed over long distances when the total number of dispersed seeds is high (Dupré and Ehrlén, 2002; Higgins et al., 2003). Small patches will favour species with high colonization ability if these patches are sufficiently connected to neighbouring patches by propagule input and populations are therefore maintained by the rescue-effect. The association between seed number and patch area was not detected in the more arid land units – Lachish and Dvir. Typically, in arid environments adaptations for long-distance dispersal are rare, while adaptations to climatic variability and/or seed predation, e.g. lignified seed containers or attachment of the seeds to the dead mother plant, restrict dispersal distance (Ellner and Shmida, 1981; Venable et al., 2008). We presume that this selection against long-distance dispersal adaptations is responsible for the absence of the associations between seed traits and habitat fragmentation in the more arid sites of the S–N gradient studied here.

In this study we used presence/absence data and thus equal species weights in the calculation of community-mean trait values instead of using relative abundances as species weights (e.g. Ackerly and Cornwell, 2007). This choice primarily reflects the fact that species abundance data were only available at the smallest sampling scale. However, there is also evidence that species presence/absence data reflect environmental gradients as good or even better then abundance data (Wilson, 2012). Furthermore, weighting species by abundance might introduce a bias towards small species, which often show considerably higher densities and thus higher relative abundances than large species. Instead, we suggest that using biomass as a weight in the calculation of community-mean traits would be of high interest and relevance for assessing the robustness and generality of the results presented here. However, due to the lack of biomass data this test could not be implemented within this study.

All associations between community-mean trait values and fragmentation indices discussed here were selected in the models with high statistical confidence. Nevertheless the effect sizes of fragmentation on community-mean traits predicted by our models were comparably low. This general finding corresponds closely to previous studies, which found that fragmentation tends to have a lower explanatory power with respect to plant functional traits than local environmental variables (Dupré and Ehrlén, 2002; Hérault and Honnay, 2005; Lindborg et al., 2012). In this context it is also important to note one conceptual and statistical key challenge in trait-based ecology. Even if there are significant associations of community-mean trait values with environmental drivers, such as productivity or precipitation, an enormous amount of trait variation is often found among species within the same community (McGill et al., 2006). For example Wright et al. (2004) found that the impressive proportion of 36% of the global variation of species' SLA occurred within sites. This indicates that there is still a need for better understanding of how local processes and factors as competition and small-scale environmental heterogeneity structure trait distributions at small spatial scales (Götzenberger et al., 2012).

In this study, we focused on inter-specific trait variation at the landscape scale within a highly diverse system. Functional traits also vary within species, but sampling intra-specific trait variation for the number of species and for the number of plots considered here, is hardly feasible. Cornwell and Ackerly (2009) found that the response of community-level traits to environmental gradients is dominated by species turnover and thus by inter-specific variation, while intra-specific variation plays a minor role. Furthermore, functional traits are expected to shift in the same direction along environmental gradients at the species and at the community level (Ackerly and Cornwell, 2007; Harel et al., 2011). Therefore, intra-specific variation in trait values is unlikely to affect our main conclusions. On the contrary, previous studies suggest the expectation that considering intra-specific trait variation would even increase the statistical power and effect sizes of the analysis presented here (Cornwell and Ackerly, 2009; Jung et al., 2010).

Conclusions

To the best of our knowledge, this study provides the first empirical test of community assembly processes and plant functional trait associations with habitat fragmentation along an abiotic environmental gradient. Our findings clearly indicate the importance of choosing appropriate null-models and species pools for studying community assembly processes (De Bello et al., 2012). Furthermore our results highlight that community ecology still lacks a predictive theory as well as empirical evidence regarding the conditions under which competition results in trait divergence by excluding species with high trait similarity, or in trait convergence by excluding species with low trait similarity (Mayfield and Levine, 2010).

With respect to trait–environment relationships, our findings closely match the results of previous studies investigating plant traits along environmental gradients and strongly suggest that habitat filtering by varying precipitation and productivity is the main driving force of trait distribution along the S–N gradient investigated here. Accordingly, we suggest that the varying associations between seed traits and habitat fragmentation are driven by the interactive effects of productivity and fragmentation on species distributions and community composition. Our findings emphasize the need to consider species adaptations to dispersal for projections of environmental change effects and, vice versa, to consider species environmental adaptations for projections of land use and fragmentation effects. In this way our study highlights the importance of addressing the interactive effects of important environmental drivers on plant functional traits in order to improve our understanding and the predictability of plant community responses to global change.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2013.08.002.

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Please cite this article in press as: May, F., et al., Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. Perspect. Plant Ecol. Evol. Syst. (2013), http://dx.doi.org/10.1016/j.ppees.2013.08.002