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The role of species pools in determining species diversity in spatially heterogeneous communities

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Abstract

1. The "habitat-specific species pool hypothesis" proposes that differences between habitats in the sizes of their species pools are the main drivers of diversity responses to habitat heterogeneity. Empirical tests of this hypothesis are not trivial as species might be missing from ecologically suitable habitats due to limited dispersal, while others may occur in unsuitable habitats by means of source–sink dynamics and mass effect.

2. We tested the habitat-specific species pool hypothesis in a local, environmentally heterogeneous community of annual plants using a novel "ecological selection" experiment. Mixtures of seeds representing the whole community were sown in each habitat, and the emerging species were exposed to six generations of selection by environmental filtering and competition while being blocked from dispersal. A comparison of the total number of species that were able to survive in each habitat (i.e. to pass the selection test) with data on species richness in the natural community allowed us to test the degree to which observed differences in species richness between habitats could be explained by differences in the sizes of the respective species pools.

3. Results supported the species pool hypothesis, showing that differences in the sizes of the habitat-specific species pools were important in determining diversity responses to habitat heterogeneity. Moreover, species richness showed a unimodal response to local-scale gradients in habitat productivity, and this response could be attributed to underlying differences in species pool sizes. Both results were robust to properties of the data and the method of analysis.

4. *Synthesis*. Our results provide a strong experimental evidence that differences in the sizes of habitat-specific species pools might be important in shaping the diversity of local communities. Future theoretical and empirical studies in community ecology should explore the potential sources and implications of such differences.

KEYWORDS
annual plants, grasslands, habitat heterogeneity, plant competition, plant population and community dynamics, productivity–diversity relationship, species diversity, species pool hypothesis

1 | INTRODUCTION

A fundamental question in plant ecology concerns the processes controlling species diversity along habitat gradients in general and productivity gradients in particular. This question is complex because such processes are multidimensional and depend on properties of both the species and the environment, as well as on the scale at which the system is examined (Dickson & Foster, 2008; Foster, Dickson, Murphy, Karel, & Smith, 2004; Laliberte, Zemunik, & Turner, 2014; Partel & Zobel, 2007; Rajaniemi, 2003; Rajaniemi, Goldberg, Turkington, & Dyer, 2006; Simova, Li, & Storch, 2013). Still, at a broad level, there are two main sources of variation in species richness between habitats: (1) variation in the nature of the interactions among species and between species and their environment; and (2) variation in the sizes of the habitat-specific species pools. Dispersal processes modify the effects of these two forces, thereby determining the manner by which these effects are "translated" into the observed patterns of species diversity (Cadotte, 2006).

Traditionally, ecologists have focused on local processes (interactions among species and between species and their environments) as the main drivers of diversity responses to differences in habitat conditions (Hutchinson, 1957; Tilman, 1982). Later, this local-scale perspective has been extended to incorporate the potential effects of dispersal processes (Chave, Muller-Landau, & Levin, 2002; Gravel, Canham, Beaudet, & Messier, 2006; Mouquet, & Loreau, 2003; Shmida, & Wilson, 1985). Only more recently, and particularly since the seminal work of Ricklefs (1987) on the roles of local vs. regional processes of species diversity, more attention has been paid to species pools as determinants of species diversity (see Cornell, Harrison, & Futuyma, 2014; Partel, Bennett, & Zobel, 2016; Zobel, 2016 for recent reviews). However, empirical tests of the degree to which regional species pools are important in determining local species richness are not trivial because, in contrast to local richness which is an unambiguous concept, a "regional species pool" is an abstract concept, and therefore more difficult for empirical quantification. Still, there is a growing evidence that differences in species richness between plant communities are at least partially driven by underlying differences in the sizes of the respective species pools (Algar, Kerr, & Currie, 2011; Dupre, Wessberg, & Diekmann, 2002; Houseman & Gross, 2006; Myers & Harms, 2009; Partel, Zobel, Zobel, & van der Maarel, 1996; Rajaniemi et al., 2006; Safford, Rejmanek, & Hadac, 2001; Simova, Li, & Storch, 2013).

These studies confirm that processes operating over evolutionary or historical scales may influence the structure of local communities.

Evolutionary processes may also lead to differences in species pools among habitats within the same region, e.g. due to differences in the spatial extent of the habitats in which they have evolved (Taylor, Aarssen, & Loehle, 1990). Quantifying such "habitat-specific species pools" (Zobel, 2016) might be even more challenging than the quantification of "regional species pools," as most habitats do not have clear boundaries, and any definition of a "habitat" has a subjective element. Moreover, in natural communities, species might be missing from ecologically suitable habitats due to dispersal limitation (Hubbell et al., 1999; Partel & Zobel, 2007), while other species may occur in unsuitable habitats by means of source–sink dynamics (Kadmon & Shmida, 1990) and mass effect (Kunin, 1998). Such dispersal related processes further complicate the identification of habitat-specific species pools.

Here we report the results of a long-term study that was designed to test the habitat-specific species pool hypothesis in a spatially heterogeneous community of annual plants. A unique feature of our study is the use of a multi-generation "ecological selection" experiment for quantifying the habitat-specific species pools. The main idea behind this approach was to identify the species pools of different habitats (i.e. the "habitat-specific species pools") by sowing mixtures of species representing the species pool of the whole community in different habitats, and exposing them to several generations of "ecological selection" by environmental filtering and competition while being blocked to dispersal (in order to prevent contamination by seeds of species growing in other habitats). Thus, "selection" in the experiment refers to the process of habitat-specific elimination of ecologically unsuitable species from the original species pool during the course of the experiment. A comparison of the total number of species that were able to survive in each habitat (i.e. to pass the selection test) with measurements of species richness in plots representing the natural community, allowed us to test the degree to which observed differences in species richness between habitats could be explained by underlying differences in the sizes of the habitat-specific species pools. Importantly, we assume that habitat-specific species pools are determined by evolutionary or historical processes, and can be considered constant over the time-scale of the experiment.

We applied our experimental approach in a community of annual plants where local-scale differences in soil-depth are a major source of habitat heterogeneity (Figure 1). This system was particularly suitable for our purpose for two reasons. First, differences in soil-depth
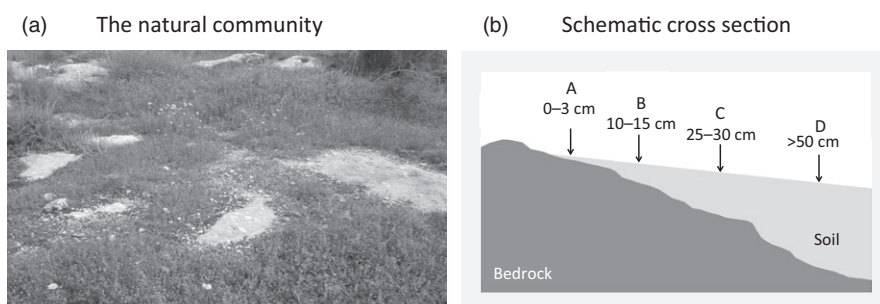
(a) The natural community

(b) Schematic cross section

FIGURE 1 The study system. (a) A photo showing typical soil-depth gradients in the study community. (b) A schematic illustration of a local gradient in soil-depth and the soil-depth categories used as "habitats" in the study

occurred over very small distances (<1 m), ensuring that plots representing different "habitats" are exposed to the same "seed rain". We distinguished between three hierarchical levels of species diversity in the study system: the regional species pool (the total number of species in the community), the habitat-specific species pools (those species capable of tolerating the abiotic and biotic conditions in the relevant "habitats") and plot richness (the species actually present in a small (20 × 20 cm) plot, where plots are nested within habitats). Importantly, habitat-specific species pools represent "filtered" pools (sensu Cornell et al. 2014) in the sense that they are defined based on the realized niches of the species, including their ability to persist at the presence of potential competitors (Cornell et al., 2014, Zobel, 2016; Partel, Bennet, & Zobel, 2016).

An additional advantage of the study system was that local gradients in soil-depth generate related gradients in above-ground biomass (i.e. productivity in the case of annual plants, Figure 1a, Figure S1). This feature allowed us to utilize our study as a test of the long-standing debate concerning the mechanisms responsible for the unimodal response of species richness to productivity gradients (Grace, Adler, Harpole, Borer, & Seabloom, 2014; Grime, 1973; Newman, 1973). Although many hypotheses have been proposed as possible explanations for this pattern (Abrams, 1995; DeMalach, Zaady, Weiner, & Kadmon, 2016; Grime, 1973; Groner & Novoplansky, 2003; Kondoh, 2001; Newman, 1973; Partel & Zobel, 2007; Rajaniemi, 2003; Xiao et al., 2010), a major debate focuses on the role of local processes vs. differences in species pool sizes (Houseman & Gross, 2006; Safford, Rejmanek, & Hadac, 2001; Taylor, Aarssen, & Loehle, 1990). We therefore designed our experiments to test two related hypotheses: (1) that differences in habitat-specific species pools are important in determining diversity responses to habitat heterogeneity and (2) that such differences may explain the unimodal response of species diversity to productivity gradients.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted within an area of about 4 ha at the centre of the Beit Guvrin National Park, Israel (31°36′01″N, 34°53′55″E). Mean annual precipitation is about 420 mm, falling between November and April. This area is situated 270–300 m above sea level and is characterized by a hilly topography and scattered rock outcrops that create sharp gradients of soil-depth ranging from a few millimetres (at outcrops edges) to more than 50 cm (away from outcrops and at the bottom of the slopes). The vegetation is dominated by annual plants (in terms of abundance, richness and biomass), with grass species comprising most of the biomass and forb species comprising most of the taxonomic diversity. Most grass species are taller than forbs in the study area, a pattern confirmed by height measurements of individual species growing under controlled greenhouse conditions (DeMalach et al., 2016). Due to the annual nature of the vegetation, gradients in above-ground biomass can be interpreted as productivity gradients (Figure S1, see also DeMalach, Zaady, & Kadmon, 2017; Segre et al.,

2014). A complementary mesocosm experiment of ecological selection under more controlled conditions was conducted at the Hebrew University Botanical Garden, Jerusalem, using seeds collected in the field (see below). Both experiments were conducted in fenced areas protected from grazing by large herbivores and there were no signs of other sources of herbivory in the experimental plots.

2.2 | Field sampling

The aim of the sampling component of the study was to obtain data on the response of the natural community to differences in soil-depth. Based on preliminary observations, four soil-depth categories (hereafter termed "habitats") were defined in advance to represent the range of soil-depth in the study area (Figure 1): 0–3 cm (A), 10–15 cm (B), 25–30 cm (C) and ≥50 cm (D). Measurements of soil nutrient concentration (NO_3, NH_4 and P) revealed small and non-significant differences between shallow (0–20 cm) and deeper (20–40 cm) soil layers (NO_3: 5.0 vs. 4.4 mg/kg; NH_4: 29.7 vs. 27.9 mg/kg; P: 9.3 vs. 8.9 mg/kg respectively), suggesting that nutrient availability was approximately proportional to soil-depth.

Plots of 20 × 20 cm representing each soil-depth category were identified by hammering a measuring metal rod (6 mm in diameter) into the ground in randomly located points until it reached the hard bedrock surface. The rod was inserted three times within each plot in order to identify plots with homogeneous soil-depths. The scale of 20 × 20 cm was chosen because soil-depth at this scale was relatively uniform. Distances between neighbouring plots were larger than the scale of patchiness in rock outcrops (at least 2–3 m apart) in order to prevent spatial autocorrelation in soil-depth. In April 2010, we sampled the vegetation in plots representing the four soil-depth categories. Thirty plots were identified in each "habitat" and all vascular species occurring within each plot were determined. Based on these data, we quantified two measures of richness for each plot: "plot absolute richness" (the total number of species observed in the plot) and plot resident richness (the number of species that were classified as "residents" in the relevant habitat, see below). We also determined the above-ground biomass of each soil-depth category using samples of 20 × 20 cm that were dried for 10 hr at 105°C.

2.3 | Field experiment

The aim of the field experiment was to obtain the data required for determining the species pools of the four habitats. This part of the study was based on the following procedure (see Appendix S1 for technical details): (1) samples of the soil seed bank representing the four habitats were collected and mixed together in order to create a homogeneous mixture representing the regional (community-level) species pool; (2) Random samples from this mixture were sown in 10 experimental plots representing each of the four habitats following removal of the above-ground biomass and original seed bank from these plots; (3) the species emerging within the plots were allowed to grow and interact with each other for six generations (2011–2016); (4) during the dispersal period of each year the plots were blocked

from dispersal (both immigration and emigration) using 50-mesh vertical nylon nets; and (5) at the end of the experiment (December 2016), all species survived in each plot were identified.

The species that survived in the experimental plots of a given habitat at the end of the experiment were considered potential "resident" species in that habitat. The corresponding habitat-specific species pool was determined by intersecting the list of potential residents with the list of all species recorded in the sampling component of the study (i.e. those species that were observed in both the sampling plots and experimental plots of the relevant habitat). The regional species pool was determined as the union of all habitat-specific species pools (i.e. those species that were found in at least one habitat-specific pool).

2.4 | Mesocosm experiment

One limitation of our experimental approach is that not all species occurring in the sampling plots may necessarily be found in the experimental plots (e.g. due to rare establishment events, limited number of plots, sampling bias, etc.). As a result, some species that occur in the natural community may not be classified into any of the habitat-specific pools, resulting in underestimates of the habitat-specific species pools. To evaluate the robustness of our results to such "incomplete detection," we performed a complementary outdoor "mesocosm" experiment in which we sowed seed mixtures of 51 species (Table S1) representing a wide range of taxa, functional groups, soil specificity (both specialists and generalists, based on distribution along the natural soil-depth gradient), and commonness (both common and rare species) in large (1 × 1 m) containers representing the four soil-depth categories used in the field. These mesocosm "communities" were exposed to 5 years of ecological selection (2011–2016) in parallel to the field experiment. Each soil-depth category was represented by nine containers that were randomized to provide a completely random design (a total of 36 containers). The containers were sown at a density of 200 seeds per species (a total of 10,200 seeds per container) and were blocked from dispersal during the dispersal periods of the 5 years. The species surviving at the end of the experiment in containers representing a given soil-depth category were considered as potential residents of that category (see Appendix S2 for more technical details).

2.5 | Data analysis

2.5.1 | Distinguishing between habitat-level and plot-level filtering

The basic hypothesis tested in this study was that differences between habitats in species pool sizes are important in determining local-scale differences in species richness. We tested this hypothesis by distinguishing between two levels of diversity limitation—the habitat level and the plot level. For each level, we quantified the magnitude of diversity limitation using two alternative measures: "relative richness" and "completeness". Both measures can be used to quantify

the magnitude of reduction in the number of species from one level in a hierarchy of scales to a lower level.

Relative richness is a proportional measure expressing the number of species observed in a given scale as a fraction of the number observed at some larger scale (Cam, Nichols, Sauer, Hines, & Flather, 2000; Chocron, Flather, & Kadmon, 2015; Partel, Helm, Reitalu, Liira, & Zobel, 2007). In this study, we calculated two levels of relative richness—"habitat-relative richness" (the ratio between the number of species in a habitat-specific pool and the number of species in the regional pool) and "plot relative richness" (the ratio between the number of resident species in a plot and the number of species in the respective habitat-specific species pool).

While relative richness has the advantage of being simple and intuitive, recent studies have advocated the use of an alternative measure based on the log-ratio of observed/"dark" diversity. This measure (termed "completeness," Partel, Szava-Kovats, & Zobel, 2013) can be quantified for any pair of nested spatial scales (habitats within a region, plots within a habitat, etc.), and indicates the (log) ratio between the number of species observed at the smaller scale and those that are absent from the smaller scale, but do occur at the larger scale (referred to as "dark" diversity, Partel, Szava-Kovats, & Zobel, 2011). In contrast to relative richness, the log-ratio is not confined to a limited range of values and ranges from $-\infty$ to $+\infty$.

As with the measure of relative richness, we calculated two levels of completeness: "habitat completeness" (the log-ratio between the number of species in a habitat-specific specie pool and those that were present in the regional pool but not in the habitat-specific pool); and "plot completeness" (the log-ratio between the number of species in a plot and those that were present in the respective habitat-specific pool but not in that plot).

2.5.2 | Evaluating sensitivity to potential sources of bias

As emphasized above, incomplete detection of species in the field experiment may lead to negatively biased estimates of habitat-specific species pools. To evaluate the sensitivity of the patterns observed to such bias, we quantified the habitat-specific pool of each habitat (soil-depth category) using two different sets of data, one based on the field experiment alone (hereafter termed the "field-based analysis") and the other based on the combination (union) of the lists of resident species obtained from the field and mesocosm experiments (hereafter termed the "combined analysis"). We expected that the combined analysis will show larger sizes of species pools, but will not differ from the field-based analysis in the qualitative patterns of among-habitat variations in species diversity.

While incomplete detection of "resident" species may introduce a negative bias into estimates of habitat-specific species pools, other factors may lead to a positive bias in such estimates. For example, small fitness differences among species, environmental fluctuations, low rates of competitive exclusion and long-lived seed banks, may all slow the rates of ecological selection, thereby allowing non-resident species to survive in plots of an unsuitable habitat for long periods. In

the present study, we attempted to minimize such bias by continuing the experiment for six generations while preventing opportunities for immigration. However, even such period may not guarantee complete extinction of non-resident species in unsuitable plots.

To evaluate the robustness of our results to such positive bias, we performed an additional set of analyses in which only species occurring in at least 20% of the experimental plots (in the case of the field experiment) or 20% of the containers (in the case of the mesocosm experiment) were included in the analysis. We considered the later analysis (hereafter "common-species analysis") more conservative in the sense that it was expected to reduce the likelihood of "false positive" errors in estimates of the habitat-specific species pools. This analysis was conducted using the union of the lists of resident species obtained from the two experiments (i.e. the "combined analysis") in an attempt to minimize both types of errors. We expected that the common-species analysis would show smaller sizes of habitat-specific species pools than both the field-based analysis and the combined analysis, but should not differ from the two other analyses in the qualitative patterns of diversity responses to the soil-depth gradient. Thus, all our statistical analyses (see below) were repeated using three different approaches for estimating the habitat-specific species pools: "field-based analysis," "combined analysis" and "common-species analysis".

2.5.3 | Statistical analysis

Differences between habitats (soil-depth categories) in the sizes of the habitat-specific species pools were analysed using randomization tests with the null hypothesis that each species in the regional species pool has the same probability to occur in each of the four habitats. To perform such randomization, we summarized the lists of habitat-specific species pools obtained for the four habitats as a habitat × species matrix of presence/absence data, and randomized the matrix keeping the number of presences per species as in the observed matrix. Such permutations were repeated 10,000 times, and for each permutation, we recorded the absolute difference in the number of species between each pair of habitats. The distribution of differences obtained for each pair of habitats under this null model was compared with the respective observed difference, in order to determine the relative frequency of model permutations that produced a difference that was equal to, or exceeded, the observed difference. This value was interpreted as the significance level of the observed difference. Such significance levels were computed for each pair of habitats. A similar randomization procedure was applied to determine the statistical significance of differences in habitat-level completeness. This analysis had three steps. First, we calculated the value of habitat-level completeness for each habitat in each of the 10,000 permutations. Based on these values, we constructed a null distribution of differences in habitat completeness for each pair of habitats. These null distributions were compared with the respective observed differences in order to determine their significance levels.

Differences in plot-level diversity between habitats were analysed using three types of response variables: plot absolute richness, plot relative richness and plot completeness. For each measure,
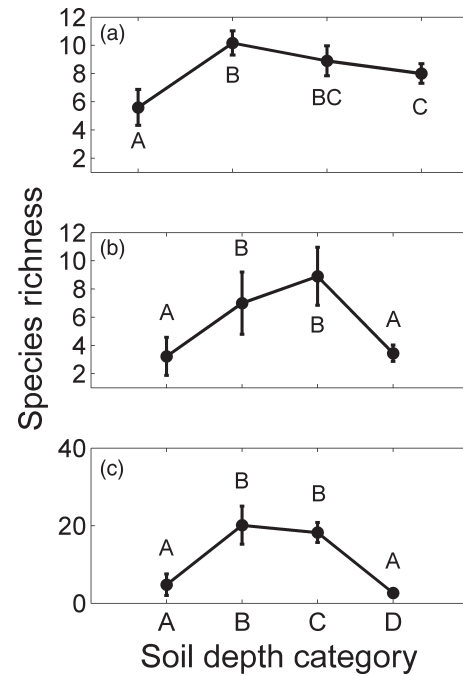

FIGURE 2 Response of species richness to variation in soil-depth. (a) Sampling of the natural community; (b) Field experiment; and (c) Mesocosm experiment. Soil-depth categories: (A) 0–3 cm; (B) 10–15 cm; (C) 25–30 cm; and (D) ≥50 cm. Error bars represent 95% confidence levels. Common letters indicate soil-depth categories that do not differ significantly based on Tukey's post hoc tests

we performed one-way ANOVA test with plots as sampling units and habitats as a main (fixed) effect. Values of plot relative richness were arcsine-square-root-transformed to stabilize the variance. Furthermore, Tukey's post hoc tests were performed for comparing pairs of habitats.

3 | RESULTS

Species richness in both the sampling plots (Figure 2a) and the experimental plots (Figure 2b) showed a unimodal response to the soil-depth gradient. This unimodality was statistically significant in the sense that values of species richness at both ends of the gradient were significantly lower than the values obtained for at least one of the intermediate soil-depths. The fact that initial conditions in the field experiment were uniform across all soil-depth categories (all plots were sown using equivalent samples of the regional species pool) suggests that this unimodality was causally related to the differences in soil-depth.

The response obtained in the mesocosm experiment was also unimodal and statistically significant (Figure 2c). In this experiment, all containers had exactly the same substrate and were sown using the same species and the same amount of seeds per species, confirming the causality of the observed relationship between species richness and soil-depth.

Variations in the sizes of the habitat-specific species pools and plot resident richness were also significantly unimodal under all analyses
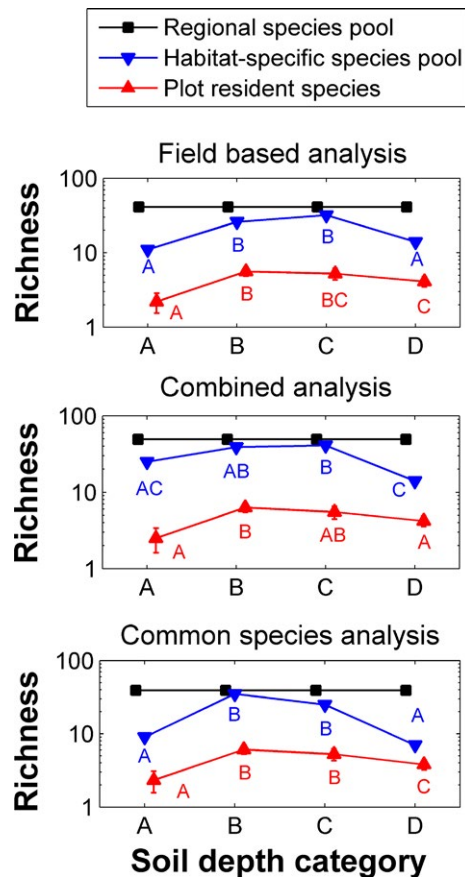
FIGURE 3 Effect of soil-depth on the sizes of the habitat-specific species pools (blue) and mean (±95% CI) plot resident richness (red). Analyses were performed using three different estimates of the habitat-specific species pools: field-based analysis, combined analysis and common-species analysis (see Materials and Methods). The size of the regional species pool is also shown as a reference (black). Soil-depth categories: (A) 0–3 cm; (B) 10–15 cm; (C) 25–30 cm; and (D) ≥50 cm. Common letters indicate soil-depth categories that do not differ significantly (randomization tests for habitat-specific species pool sizes and Tukey's post hoc tests for plot resident richness) [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 3). However, the magnitude of the decline in plot resident richness at greater soil-depth (soil-depth D) was much weaker than the corresponding decline in the size of the habitat-specific species pool (note the logarithmic scale). This difference between the magnitudes of habitat-level and plot-level declines was consistent over all analyses (Figure 3).

As could be expected from these results, habitat-relative richness and plot relative richness showed different responses to the soil-depth gradient (Figure 4a). While the patterns obtained for habitat-relative richness were consistently unimodal, the patterns obtained for plot relative richness were relatively uniform across the lower soil-depth categories (soil-depths A–C) but showed a significant increase towards the deepest soil (soil-depth D). Thus, plots representing the deepest soils had significantly smaller species pools than those representing intermediate soil-depths, but showed a more complete representation of the underlying habitat-specific species pools than the latter plots.

Similar results were obtained when differences in the magnitude of species filtering between habitats were analysed using the log-ratio measure of completeness (Figure 4b), supporting the robustness of this result.

4 | DISCUSSION

Using a novel experimental approach for determining habitat-specific species pools in annual plant communities, we show that (1) habitats representing different positions along a soil-depth gradient differ significantly in the sizes of their species pools and (2) these differences are responsible for the unimodal response of species diversity to productivity gradients. These findings provide a strong support for the habitat-specific species pool hypothesis. Below we discuss the implications of these findings for our understanding of the factors regulating species diversity in general and diversity responses to productivity gradients in particular.

4.1 | Methodological considerations

In most previous tests of the species pool hypothesis, the size of the species pool was quantified based on observational data, usually the list of species that were observed in the relevant habitat or relevant region, sometimes with further modifications based on ecological traits (Partel et al., 1996), species-accumulation curves (Safford, Rejmanek, & Hadac, 2001) or rarefaction methods (Laliberte et al., 2014). While this approach might be reasonable at large spatial scales, it ignores the potential effects of dispersal processes that may be particularly important at the scale of a local community (Amarasekare, 2003; Cadotte, 2006). Most importantly, it may overestimate the sizes of habitat-specific species pools by considering "non-resident" species maintained by "source–sink" dynamics (Pulliam, 1988) and "mass effect" (Shmida & Wilson, 1985) as belonging to the species pools of the habitats in which they are observed. This problem is particularly acute if neighbouring habitats are in close proximity to each other and is intensified by differences between habitats in ecological conditions and species pool sizes. For example, the contribution of mass effect to the observed diversity of a given habitat might depend on the difference in ecological conditions between the two habitats (the intermediate difference hypothesis, Kunin, 1998). Similarly, a habitat with a large species pool can be expected to have a stronger mass effect on the diversity of a species-poor habitat than vice versa. The spatial configuration of neighbouring habitats may also affect the degree to which they are influenced by mass effect. Surprisingly, most previous tests of the species pool hypothesis have ignored the potential effects of such dispersal processes, even if focused on relatively small spatial scales (though see Cantero, Partel, & Zobel, 1999).

In this study, we quantified habitat-specific species pools using an alternative, experimental approach, in which propagules representing the overall community are sown in plots representing the relevant habitats and are exposed to several generations of ecological selection by
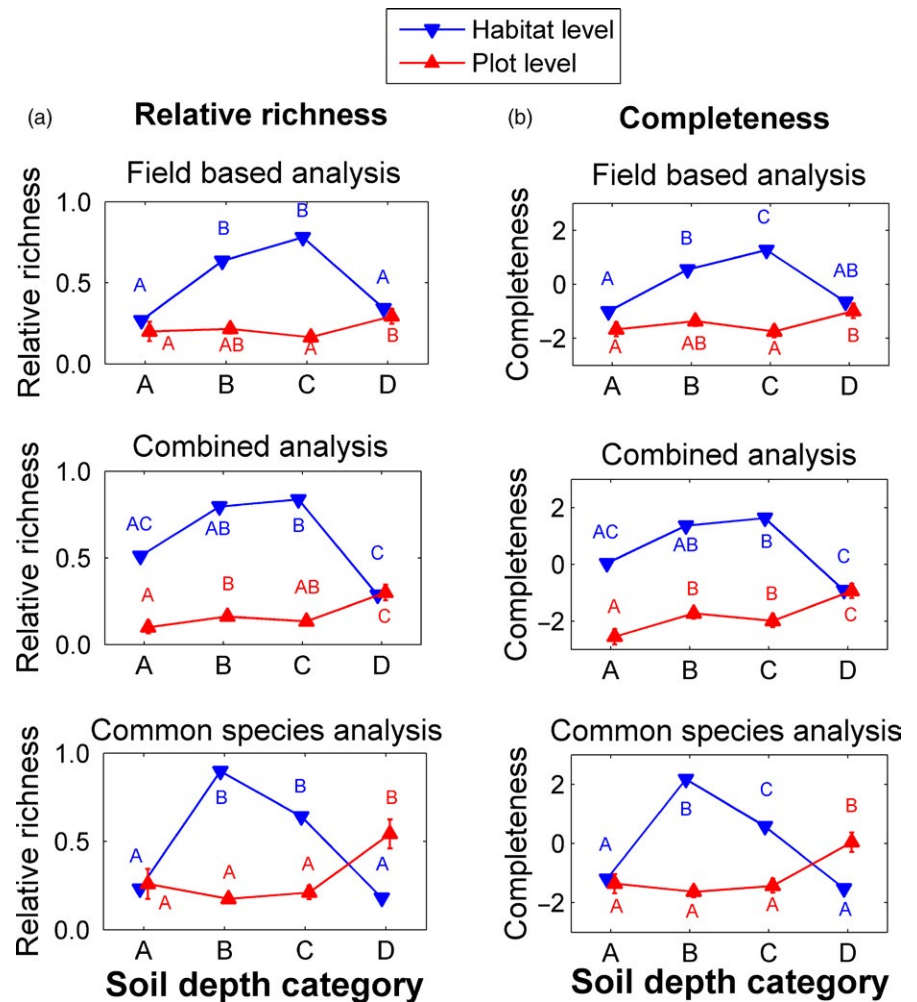
FIGURE 4 Effect of soil-depth on habitat-level (blue) and plot-level (red) filtering, quantified using relative richness (a) and completeness (b). Analyses were performed using three different estimates of the habitat-specific species pools: field-based analysis, combined analysis and common-species analysis (see Materials and Methods for full description). Soil-depth categories: (A) 0–3 cm; (B) 10–15 cm; (C) 25–30 cm; and (D) ≥50 cm. Common letters indicate soil-depth categories that do not differ significantly (randomization tests for habitat-level measures and Tukey's post hoc tests for plot-level measures) [Colour figure can be viewed at wileyonlinelibrary.com]

all abiotic and biotic filters that operate at the plot scale. Importantly, such selection incorporates direct competition with other species included in the regional species pool, thereby fitting the concept of a "filtered" species pool (Cornell et al., 2014; Partel et al., 2016; Zobel, 2016). We therefore believe that our experimental approach provides more reliable estimates of habitat-specific species pools than the common observational approach.

Still, as in any experiment, our approach has inherent limitations imposed by the spatial and temporal scales at which the experiment is conducted. Most importantly, slow rates of ecological selection (e.g. due to long-lived seed bank, small fitness differences or environmental fluctuations) may cause a positive bias in estimates of the habitat-specific species pools by allowing non-resident species to persist in the plots as "sink" populations for long time periods. In this study, we attempted to minimize such bias using two complementary approaches. First, we conducted the experiment over six generations using an experimental setup of a "closed community" (no immigration or emigration) in order to increase the effectiveness of filtering by both abiotic conditions and competition. Although 6 years may not guarantee a complete exclusion of non-resident species, the large differences observed between the numbers of species germinated in the first year of the experiment and the numbers observed

in the last year (Figure S2) suggest that the temporal extent of the experiment was sufficiently long to cause considerable selection in the study communities. It can also be seen that the difference in species numbers between the first and last counts increased with soil-depth, indicating that the decrease of species diversity towards the shallowest soil-depth was due to limited emergence in the first year of the experiment. This result suggests that abiotic stress (rather than competition) was the main force of filtering at this side of the gradient.

Second, in an attempt to further reduce the likelihood of "false-positive" errors, we repeated our analyses using a more conservative approach in which we counted only species occurring in at least 20% of the experimental plots (containers in the case of the mesocosm experiment) as resident species and the qualitative results were similar to those observed in the all-species analysis (Figure 4). We therefore believe that the qualitative patterns found in this study were robust to bias caused by the limited extent of the experiment. The similarity of the results obtained from the "field-based analysis" and "combined analysis" (Figure 4) further supports this conclusion.

An opposite source of bias (underestimating the size of the habitat-specific species pool) may arise in our ecological selection experiment if not all species occurring in the natural community are
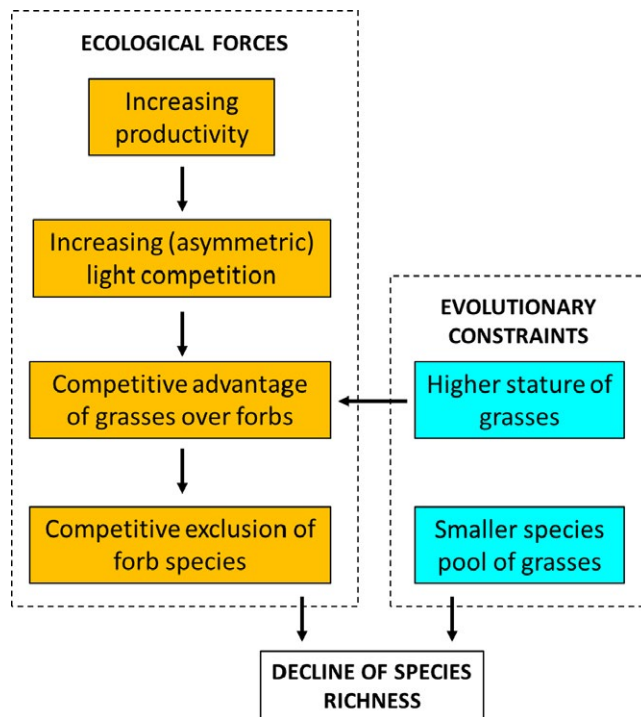
FIGURE 5 A hypothetical model of the factors responsible for the decline of species richness under high level of productivity in the study system. Orange boxes represent ecological factors and light blue boxes represent evolutionary factors. The mechanism behind species loss is competition for light (an ecological process), but the reason that this mechanism reduces species richness is that the "winners" of light competition (grasses) have a smaller species pool than the "losers" of such competition (i.e. evolutionary constraints on taxonomic diversity and functional traits) [Colour figure can be viewed at wileyonlinelibrary.com]

present in the experimental plots. However, the total number of species observed in the experimental plots during the first year of the experiment was much larger than the total number of species observed in the sampling plots (138 vs. 88 respectively). This result suggests that, in spite of the much smaller sample size in the experiment (40 vs. 120), the original composition of the species emerging in the experimental plots provided a reasonable representation of the regional species pool.

Finally, it should be noted that any quantification of species pools has an arbitrary element due to the probabilistic nature of species responses to environmental gradients (Zobel, van der Maarel, & Dupre, 1998). Clearly, species do not show binary responses to variations in habitat conditions, and the binary response assumed by classifying species to residents vs. non-residents in a given habitat is a simplification of the real world.

4.2 | Relevance to the productivity–diversity debate

Our results are highly relevant for the long-standing debate concerning the mechanisms responsible for the decline in species diversity at high levels of habitat productivity. This decline has originally been attributed to an underlying increase in the intensity of light competition

(Newman, 1973; see DeMalach et al., 2017; Lamb, Kembel, & Cahill, 2009 for empirical tests), but an alternative hypothesis attributes it to differences in the sizes of the respective species pools (Taylor, Aarssen, & Loehle, 1990). Empirical attempts to discriminate between the two views were mostly based on statistical analyses of observational data (e.g. Simova, Li, & Storch, 2013) and seed addition experiments (e.g. Houseman & Gross, 2006). The general pattern emerging from such studies is that both kinds of factors are involved in causing the decline of species diversity in highly productive habitats (Fraser et al., 2015; Freestone & Harrison, 2006; Houseman & Gross, 2006; Laliberte, Zemunik, & Turner, 2014; Myers & Harms, 2009; Partel, Zobel, Zobel, & van der Maarel, 1996; Safford, Rejmanek, & Hadac, 2001; Simova, Li, & Storch, 2013). It has also been found that the relative importance of the two factors varies along productivity gradients with a shift from a species pool limitation to competitive limitation with increasing productivity (the "shifting limitation hypothesis," Foster et al., 2004).

Our study differs from most previous studies in its scale, its experimental approach and its main results. The spatial extent of our study (<5 ha) and the distances between plots representing different positions along the productivity gradient (a few metres) were much smaller than in most previous studies, ensuring that all plots in all habitats share the same regional species pool. Our study is also the first attempt to utilize an "ecological selection" approach as a means for quantifying the species pools of habitats representing different positions along the productivity gradient, thereby allowing us to control for potential confounding effects by other filters (e.g. habitat-specific dispersal limitation, Albert et al., 2015; Partel & Zobel, 2007; Spiegel & Nathan, 2012). Finally, and most importantly, in most previous studies, both species pools and local processes were involved in reducing richness under high levels of productivity, while in our system, the decline in richness was related to a smaller species pool, and further filtering (i.e. differences between habitats in plot-level species loss) weakened, rather than intensified the magnitude of this decline (Figure 4).

It should be emphasized, however, that the latter result does not imply that the observed decline was not related to competition. In this study, we did not quantify competitive effects, but previous experiments conducted in the same system demonstrated that competition is a highly significant driver of species loss under high levels of productivity and that the magnitude of competitive exclusion increases with increasing productivity (DeMalach, Zaady, & Kadmon, 2017; Segre et al., 2014, 2016). It has also been found that this pattern reflects a fundamental difference between grasses and forbs: grasses out-compete forb species under high productivity due to their higher stature which gives them a competitive advantage when light is the main limiting factor, but have a much smaller species pool than forb species (DeMalach, Zaady, & Kadmon, 2017). Thus, the proximate mechanism responsible for competitive exclusion at high levels of productivity is asymmetric light competition (as proposed by many previous studies), but the reason that such competition causes a decline in species diversity is a smaller pool of species capable of tolerating light competition.

Figure 5 presents a simple graphical model that illustrates this interaction between ecological and evolutionary drivers of species loss. According to this model, the decrease in species diversity at high productivity levels is caused by the interactive effects of ecological factors (asymmetry of competition leading to competitive exclusion of short species) and evolutionary factors (the fact that the species pool comprising strong light competitors is smaller). A similar trade-off between competitive ability and taxonomic diversity has been reported in other grasslands (e.g. Anten & Hirose, 1999; Noy-Meir, Gutman, & Kaplan, 1989; Xu et al., 2012) suggesting that this model can be generalized to other grassland systems.

5 | CONCLUSIONS

Previous theoretical and empirical studies on the maintenance of species diversity in spatially heterogeneous habitats have focused on the role of local interactions and dispersal processes as the main processes controlling species diversity. Our findings indicate that local interactions are indeed important in the study community, but the main reason that such interactions generate spatial variation in species diversity is underlying differences in the sizes of the habitat-specific species pools. Future theoretical and empirical studies of species diversity should pay more attention to the potential sources of differences in habitat-specific species pools and the manner by which such differences interact with habitat heterogeneity and other mechanisms in shaping the diversity of ecological communities.

AUTHORS' CONTRIBUTIONS

R.R. and R.K. conceived the ideas and designed methodology, R.R. collected and analysed the data, O.F.S. provided botanical support, R.R. and R.K. wrote the manuscript, all authors contributed to the study and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5gn79 (Ron et al., 2017).

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