Disturbed habitats locally reduce the signal of deep evolutionary history in functional traits of plants

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Summary

- The functioning of present ecosystems reflects deep evolutionary history of locally cooccurring species if their functional traits show high phylogenetic signal (PS). However, we do not understand what drives local PS. We hypothesize that local PS is high in undisturbed and stressful habitats, either due to ongoing local assembly of species that maintained ancestral traits, or to past evolutionary maintenance of ancestral traits within habitat species-pools, or to both.
- We quantified PS and diversity of 10 traits within 6704 local plant communities across 38 Dutch habitat types differing in disturbance or stress.
- Mean local PS varied 50-fold among habitat types, often independently of phylogenetic or trait diversity. Mean local PS decreased with disturbance but showed no consistent relationship to stress. Mean local PS exceeded species-pool PS, reflecting nonrandom subsampling from the pool. Disturbance or stress related more strongly to mean local than to species-pool PS.
- Disturbed habitats harbour species with evolutionary divergent trait values, probably driven by ongoing, local assembly of species: environmental fluctuations might maintain different trait values within lineages through an evolutionary storage effect. If functional traits do not reflect phylogeny, ecosystem functioning might not be contingent on the presence of particular lineages, and lineages might establish evolutionarily novel interactions.

Introduction

Present interactions among locally cooccurring plant species and their functioning within ecosystems may reflect the species' deep evolutionary ancestry (Cadotte *et al.*, 2008; Yguel *et al.*, 2016), as species sharing recent ancestors may be more similar in functional traits than species sharing only distant ancestors – a pattern named phylogenetic signal (PS) (Losos, 2008). Similarity in traits might then increase, among others, competition, and share of natural enemies or of mutualists (Yguel *et al.*, 2011; Gerhold *et al.*, 2015). It is often taken for granted that PS is strong within

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Table 1 Summary of our hypotheses and predictions.

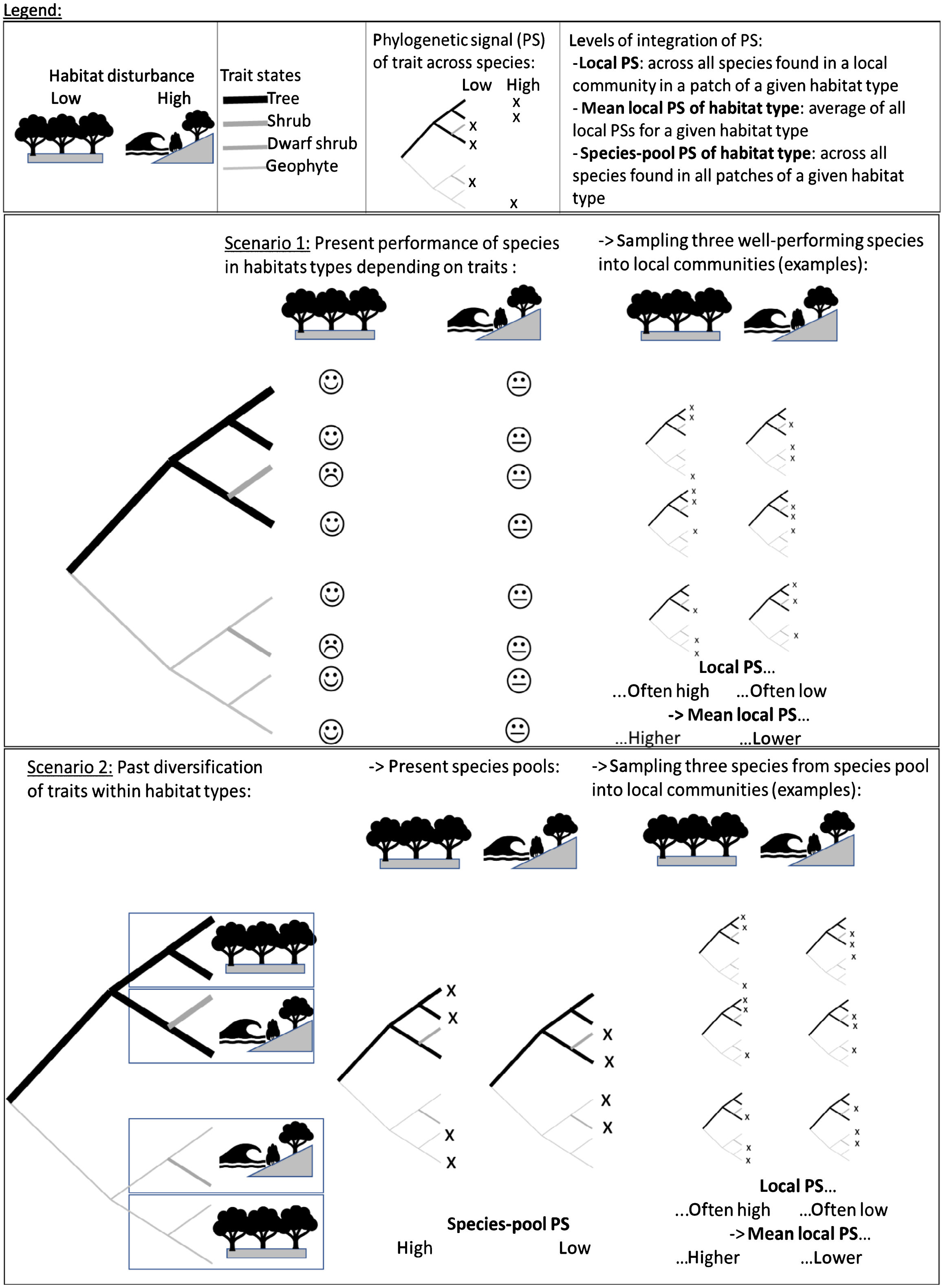
Hypothesis		Predictions on PS of habitat types	
		Mean local	Species-pool
Present local assembly of communities in different habitat types			
H1	Stress selects for specific trait values, conserved and integrated in body plans in specific lineages.	⬀ with stress	Relationships to stress/ disturbance weaker than those of mean local PSs
H2	Stress limits competition and hence local competitive replacement of related species sharing similar traits	⬀ with stress	
H3	Disturbance produces variable environmental conditions locally maintaining, within each lineage, species with traits adapted to each condition (see Fig. 1 top row)	⬂ with disturbance	
H4	Disturbances limit competition and competitive replacement of related species sharing similar traits	⬀ with disturbance	
Past diversification of traits in different habitat types			
H5–8	The above mechanisms H1–H4 operated throughout the past and influenced the diversification of species-pools in stressful or disturbed habitat types. Present mean local PSs of habitat types reflect only the PS of the corresponding habitat species-pools (see Fig. 1 bottom row for H7)	⬀ with species-pool PS (more so than phylogenetic or trait diversity)	Relationships to stress/ disturbance stronger than those of mean local PSs

local species communities, in particular by authors using the phylogenetic diversity of communities as a proxy for trait diversity or even for strong competitive exclusion (for discussion see Gerhold *et al.*, 2015). These authors argue that many traits indeed show phylogenetic signal across entire regions. However, local communities might not reflect patterns across their regional species-pools and the strength of PS has rarely been quantified for local communities (i.e. at a scale where cooccurring species are likely to truly interact, such as within tens of square metres for many plants). The few existing quantifications suggest that, locally, PS may be small and may vary greatly among local communities (Pavoine *et al.*, 2009a, 2010). What drives this major variation in local PS remains unknown. Under which conditions does past ancestry strongly relate to present functional traits and the functioning of cooccurring species, and when not?

We suggest that local PS is influenced by habitat type, as habitat types differ strongly in the degree of abiotic stress or disturbances and, as consequence, the impact of biotic interactions (Grime, 2001; Bowker *et al.*, 2010). Specifically, we hypothesize that abiotic stress might increase local PS by favouring plants with traits permitting them to cope with the stress, such as xeric stress favouring lineages with low specific leaf area or lineages with an annual life history (Ackerly, 2004; Coyle *et al.*, 2014). As a consequence, stressful conditions might favour lineages in which either of these trait values has been selected, integrated into a body plan, and conserved for many million years, rather than lineages in which these traits occur rarely, more recently or more incompletely (Ackerly, 2003; Wiens, 2008; Mayfield & Levine, 2010; Table 1, H1). In such a scenario of multiple traits favoured by stress and conserved in different lineages, stress would increase local PS. By contrast, habitats in which stress is low might trigger the competitive replacement of similar by dissimilar close relatives (MacArthur & Levins, 1967; Grime, 2001; Prinzing *et al.*, 2008; but see competitive hierarchy of Kunstler *et al.*, 2012) and thereby potentially decrease local PS (Table 1, H2).

We also hypothesize that local PS is controlled by habitat type through disturbance (Fig. 1, scenario 1). First, under frequent disturbances, access to resources is not constrained by abiotic stress, competitors or natural enemies (Grime, 2001; but see Violle *et al.*, 2010), and therefore the above described trait filtering within lineages should be weak (Ackerly, 2003; Mayfield & Levine, 2010; Kunstler *et al.*, 2012), thus decreasing local PS. Second, disturbances create fluctuating environmental conditions (Davis *et al.*, 2000), thereby maintaining species adapted to each of these conditions at some intermediate fitness (storage effects, Chesson, 2000; neutral faces in Fig. 1, scenario 1). Among species that are closely related, the presence of different unique adaptations would then reduce PS

Fig. 1 Habitat conditions drive phylogenetic signal (PS) of functional traits within local communities, and thereby whether or not the phylogenetic past relates to the functioning of species in local communities. In this example, habitat conditions are the presence or absence of disturbances (i.e. flooding). Trait states are different life forms. PS is high when differences in life forms among species reflect ancient rather than recent diversifications. Under low disturbance, access to resources is predictable and is constrained by competitors, enemies or abiotic stress, potentially increasing local PS. This may happen in two ways: first (top graph), such constraints increase the performance of species with specific strategies, often established in specific lineages. Any three such species in a local community are likely to represent the trait states of their respective lineages, that is, local PS is high. Second (bottom graph), past presence or lack of disturbances may, in addition, have influenced trait evolution within lineages, and thereby the present species-pools. In habitats lacking disturbance, species may have retained the ancestral traits of their respective lineages, that is, species-pool PS is high. Local communities sampled from these pools may reflect pool PS. Testing these scenarios requires using individual habitat types as data points, each characterized by its disturbance level, mean local PS and species-pool PS (Fig. 3; Tables 3, 4). Testing for differences among habitat types per se requires using local communities as data points, each characterized by its local PS and its habitat type (Fig. 2; Table 2).



(Table 1, H3; Fig. 1). On the other hand, under rare disturbances, biotic interactions might trigger the replacement of similar by dissimilar close relatives (Prinzing *et al.*, 2008), thereby decreasing local PS (Table 1, H4).

Stress and disturbance may affect local PS by modifying the present assembly of species into local communities in local patches of habitat types, as described above (Table 1, H1–4; example in Fig. 1, scenario 1). In addition, stress and disturbance may have also influenced the past evolution of species in the respective pools within different habitat types, given the tendency of many evolutionary lineages to only rarely leave their ancestral habitat types (Prinzing *et al.*, 2001; Crisp *et al.*, 2009). Throughout evolution, the above-discussed mechanisms – favouring or preventing coexistence among close relatives sharing similar traits – could have ultimately prevented or favoured trait divergence among close relatives in the respective habitat species-pool, thereby increasing or decreasing species-pool PS (Fig. 1, scenario 2; see Cavender-Bares, 2019 for a possible example). Today, local communities in habitat patches are sampled from these habitat species-pools and might, to some degree, reflect species-pool PSs (Table 1, H5–H8; example in Fig. 1; Gerhold *et al.*, 2018). Overall, stress and disturbance may affect local PS via both present and past effects. If present effects dominate, then local PS of habitat types should be independent of their species-pool PS, and stress and disturbance should relate to local PS within habitat types more than to PS of habitat species-pools. However, if past effects dominate, local PS of habitat types should mirror PS of their respective habitat species-pools, and stress and disturbance should relate to species-pool PS more than to local PS.

Overall, this study is the first to hypothesize mechanisms of how habitat types can affect PS independently of phylogenetic and trait diversities (Table 1). We hence predict that local communities in different habitat types show significantly different PS, and we explore which percentage of the variation of local PS among habitat types can be explained by the variation of phylogenetic and trait diversities. We then test the predictions of our hypotheses above as summarized in Table 1. For this purpose, we conducted for the first time a quantification of PS across almost all habitat types within a region, both locally and across habitat species-pools and for 10 traits. We use the Netherlands as a study system due to exceptional data availability.

Materials and Methods

Plant community data

Plant community data were taken from the Dutch National Vegetation Database containing information on the abundance of cooccurring vascular plant species in small plots within local plant communities (hereafter 'communities') across the Netherlands (available via SynBioSys, Schaminée *et al.*, 2012). For the current analyses, we retained 6704 communities containing species with the highest amount of available information (i.e. phylogenetic position and functional traits, and in sufficient numbers to perform statistical analyses; see Supporting Information Notes S1 for details on methods of selection of communities).

We defined habitat types using the highest level of Dutch vegetation classification (Schaminée *et al.*, 2012), with 43 habitat types, providing an informative but still manageable resolution of the entire spectrum of habitats representing all vegetated environmental conditions for this region. We excluded five habitat types due to insufficient sample size, as explained in Notes S1. For each of the remaining 38 habitat types, we defined the species-pool as all species in the Netherlands belonging to local communities of a given habitat type following Ozinga *et al.* (2004) and Bartish *et al.* (2010). Across habitat types, surfaces of plots had a median area of were 54 m^2, ranging from 5 m^2 for habitats dominated by the smallest herbs to 253 m^2 for habitats dominated by the largest trees (following standards in vegetation science, Schaminée *et al.*, 2012). Notes S1 provides details on the data and the sample size per habitat type.

Estimation of disturbance and stress of habitat types

Measuring all stressors or disturbances across thousands of patches of dozens of habitat types is impossible. We hence estimated disturbance and stress of different habitat types. We used two independent approaches: one based on observations of the authors of the Dutch National Vegetation Database, and one based on inference from rankings of capacities of species to live under disturbance and stress. The observation approach permits only a binary ranking (and occasionally no ranking at all), but has the advantage of being direct and entirely independent of species traits, ensuring entire numerical independence from the dependent variable, the PS of traits. The inference approach, by contrast, does permit a continuous ranking of all habitat types, but a very minor numerical dependency between mean species capacities, mean traits, and PS of traits cannot be entirely ruled out. In the Results section and Supporting Information we present both approaches and explain how they mostly give consistent results. We note that the ranking of stress and disturbance are relative to the capacities of an angiosperm from the study region. Some frost during winter, for instance, is tolerated by all species and hence not considered stress. Permanent submergence is not tolerated by most species and considered stress, even though those that do tolerated it would find lack of submergence highly stressful.

In the observation approach we classified habitat types based on their names as in the Dutch National Vegetation Database (Schaminée *et al.*, 2012). We classified 15 habitat types as being disturbed because their names indicate events that destroy biomass (Grime, 2001), acting in the past or ongoing – habitats called 'ruderal', 'disturbed', 'pioneer', 'fluctuating' or 'ephemeral' – or because the precise disturbance event is obvious from the name of the habitat type – 'floods'; mowing or grazing producing 'meadows', 'grasslands' or 'pastures' (there are no natural grasslands in the study area, except in inundated areas); 'trampling'; spring tides or storm surges in 'tidal', 'salt marsh' or 'strandline' habitats; and ploughing of 'arable' systems. We ranked six habitat types as being nondisturbed because they are 'woodlands/forests', and such vegetation cannot develop under frequent disturbance (note that the pioneer vegetation on a wind-throw is a habitat type of its own, it is not a 'forest'). We did not rank the remaining 17 habitat types as their names do not specify their level of disturbance. Concerning stress, we ranked 16 habitat types as being stressful because their names refer to a particular environmental stress such as lack of oxygen in aquatic habitats ('floating', 'submerged'); nutrient poverty ('sandy' or 'poor' or 'peat' or 'heath'); low pH ('peat' or 'heath'); harsh microclimate ('sunny wall'); or salinity ('salt', 'coastal', 'tidal', 'halophyte'). We ranked

18 of the remaining habitats as being not stressful. We refrained from ranking habitat types where some kind of stressor was mentioned in the name, but without being excessive: moisture in 'swamps' or 'periodically flooded' (but not permanently submerged/flooding); drought in 'xero' habitat types (but within the overall humid context of the Netherlands); and low pH in 'acidophilous broadleaved forests' (but being less acid than gymnosperm forests). The full list of ranks is available in Notes S2 Table A. In total, 18 habitat types could be ranked for both, stress and disturbance. Among the 18 habitat types, stressful conditions always corresponded to disturbed conditions, such as through inundations in the case of stress through saline or aquatic conditions. With this approach we hence compared stressful to unstressed habitats under disturbed conditions, and disturbed to undisturbed habitats under unstressed conditions.

In the second approach to estimate stress and disturbance, the inference approach, we inferred local stress and disturbance from the capacity of local plant species to cope with stress or disturbance of any type. Ranking these capacities, in turn, was based on Grime's (2001) CSR theory. Using plant traits, this system ranks every plant species and allows inference of the relative levels of stress and disturbance of a community from the plant's point of view (i.e. the environment to which the species is adapted). The ranking for disturbance 'R' (for 'ruderality', *sensu* Grime, 2001) was extracted from the database BIOLFLOR (Klotz *et al.*, 2002) and was available for a total of 905 out of 984 species in the dataset. We ranked species as nonruderal (0) a mixture of ruderal with two (1) or one alternative strategy (2), or solely ruderal (3). The equivalent ranking was applied for stress tolerance. From each of these two rankings, we calculated means among species at two levels: for each local community, and across local communities per habitat type ('mean local'). We used all 6505 communities with S and R ranks available for at least one species. Results per habitat type are given in Notes S2 Table B.

The observational and the inference approaches gave consistent results: habitat types whose names indicate disturbance or stress had higher scores of our disturbance or stress ranking based on plant strategies (respectively, $n = 21$; Mann–Whitney U-test $Z = 1.82$ $P_1 = 0.033$; $n = 24$; MWU $Z = 3.98$, $P_1 < 0.001$). High stress rankings, however, were very strongly related to low species richness, in particular for the inference approach ($F = 18.6$ vs $F = 12.8$ for the observation approach, accounting for habitats for which observational classifications for both stress and disturbance were available).

Traits

For each species, we extracted the values of 10 functional traits relevant to community assembly and ecosystem functioning (e.g. Kunstler *et al.*, 2016) from two complementary databases, namely Biolflor (Klotz *et al.*, 2002) and Leda (Kleyer *et al.*, 2008): flowering duration, flowering date, reproduction type, breeding system, seed mass, seed shape, life form, specific leaf area (SLA), leaf dry-matter content (LDMC) and maximum height. The number of species with trait data varied between 820 and 982 (984 species in total). Notes S3 provides definitions of traits and Notes S1 Table A gives number of species per trait. To compute the functional distances, we used the Euclidean distance for quantitative traits (i.e. flowering duration, seed mass, seed shape, SLA, LDMC, canopy maximum height) and for ordinal traits (i.e. reproduction type, breeding system or life form). We treated the trait flowering date as circular using a 'circular transformation' (Pavoine *et al.*, 2009b).

Phylogenetic signal and diversity

We characterized the evolutionary relationships between all native species through a recent, dated phylogeny of all 1283 species of Dutch angiosperm flora (excluding hybrids, subspecies and exotics; Tree Base ID S13572). The data on sequences of genes, fossil calibrations and specific analyses used to reconstruct this phylogeny have been more thoroughly described in Hermant *et al.* (2012) and Bartish *et al.* (2016). This phylogeny is consistent with, but regionally more representative than, the phylogeny of Zanne *et al.* (2014). Among others, our phylogeny is resolved within the older genera (> 35 million years old). As a result, the overall resolution of our phylogeny is 58%, a resolution that permits reliable conclusions (Notes S4).

Trait data were available at the species level and hence intraspecific taxa were considered as populations of the same species (verifying that none of the plots contained multiple intraspecific taxa of the same species), including 88 subspecies belonging to 51 species, and 12 varieties belonging to eight species. We checked the synonymy between the species names of this phylogeny and the Dutch vegetation database by using TNRS (as above) and the National Inventory of the Natural Heritage from the French National Museum of Natural History (INPN: http://inpn.mnhn.fr). Contrary to Hermant *et al.* (2012) and Bartish *et al.* (2016), our phylogeny includes the 89 exotic species found in our plots because these exotics participate in local community assembly and contribute to PS within lineages. We note, however, that the percentage of exotic species does not affect the conclusion of our study, that is that disturbed habitats have significantly or marginally significantly lower local PS of 10/10 traits and stressful habitats have higher local PS of 6/10 traits (see Results, observational approach). After including local percentage of exotic species as a covariate all these relationships remained significant or marginally significant at $P < 0.08$.

We measured phylogenetic diversity as the mean phylogenetic distance (MPD), which is the average observed pairwise phylogenetic distance (in million years) among species (Webb *et al.*, 2002), weighted by their abundance (distances did not show major gaps due to the absence of gymnosperms in our communities). We measured MPD for each local community using the R package PICANTE (v.1.6-1), and averaged its values for each habitat type (Kembel *et al.*, 2010). We also calculated standardized effect sizes (SESs) of MPD as (observed MPD − mean null MPD)/(standard deviation of null MPD), where null MPD was calculated by redistributing species 999 times across communities, keeping the species richness of communities constant (Webb *et al.*, 2002). MPD and SES MPD were highly correlated ($r = 0.71$, $P < 0.000001$). Moreover, using SES MPD instead of

MPD to explain PS of a trait (as listed in Notes S3) led to the same conclusion: explanatory power is very limited, in 7/10 traits even more limited than the explanatory power of MPD. We hence chose to present MPD, consistently with our other community measures not being SESs either (but note that species richness was accounted for in statistical analyses, and the linearity of relationships to species richness was verified graphically).

To quantify PS, we used a modified version of the tips/root skewness test by Pavoine *et al.* (2010), Pavoine (2020); details are given in Notes S1. In short, in our phylogenetic tree, each internal node supports at least two clades that descend from it. The average differences in traits (or divergence in traits) between the clades that descend from an internal node can be named a between-clade trait-based diversity. Pavoine *et al.*'s S3 statistic is bounded between 0 and 1. It quantifies the amount of association between the trait-based diversity between the clades that descend from an internal node and the distance from this internal node to the root of the tree. S3 approaches 1 (resp. 0) if the phylogenetic signal is minimal (resp. maximal), which corresponds to an increase (a decrease) in between-clade trait diversity from the root to the tips. We thus used 1 − S3 as a measure that increases with phylogenetic signal. Pavoine *et al.*'s S3 statistics of phylogenetic signal can handle any statistical type of traits (nominal, quantitative, ordinal, binary, circular etc.). It is thus particularly interesting in studies that include different statistical types of traits. The most frequently used tests of phylogenetic signal rely on a Brownian motion evolution of traits. As part of our traits are ordinal with few levels, we do not expect that these traits, coded as ordinal, follow a Brownian model (such as Blomberg's K; Blomberg *et al.*, 2003). For this reason, the advantage of Pavoine *et al.*'s S3 statistics of phylogenetic signal is that, as explained, it measures the statistical association between clade trait-based diversity at a given node and the distance of this node to the root of the tree. This statistical association is measured independently of any evolutionary model. It also has the advantage of being bounded between 0 and 1 and these limits are independent of the shape and height of the phylogenetic tree considered. Finally, the S3 statistics has been found to be more powerful and consistent to detect PS than other indices (Bennett & Cahill, 2013).

Trait functional diversity

We measured functional diversity for each trait separately, using Rao's Q (Botta-Dukat, 2005). This index measures the average functional distance between any two species weighted by their abundance using the same formula as MPD but replacing phylogenetic distances by functional distances between species. Distance matrices and Rao's Q were calculated using the functions DIST.KTAB (Pavoine *et al.*, 2009b) and DIVC of the R package ADE4 v.1.6-2 (Thioulouse *et al.*, 2018), respectively.

Statistical analyses

We stress that each local vegetation plot is only a snapshot of the local community, limited to the species present at a given moment, during a given season and at a given year. A local plot that is species-poor risks being a highly incomplete sample of the local community, and different species-poor plots could give very different estimates of PS. This is what we actually found: local PS varied most strongly among local plots of low species richness, both for real plots (Notes S5) and for simulated local plots assembled by randomly sampling different numbers of species from the regional pool (Notes S6). Such variance heterogeneity would result in a richness bias in analyses using local plots individually. This bias disappears once means across local plots are calculated within each habitat type: mean local PS did not vary most strongly among habitat types of low mean local richness (Notes S5). Later analyses hence used such means across local plots within each habitat type as data points, except for an initial ANOVA showing that PS in local plots differed significantly among habitat types (see Gerhold *et al.*, 2011 for similar between-habitat analyses).

First, we explored to what degree the mean local PS of a given trait in different habitat types can be statistically explained by the mean local Rao diversity of the same trait and by mean local phylogenetic diversity as independent variables in multiple linear regression analyses. Second, we explored to what degree the mean local PS of a given trait in different habitat types can be statistically explained by PS of the same trait within the corresponding regional habitat species-pools using Pearson's correlation across habitat types.

We then tested the predictions on statistical effects of stress and disturbance on PS and the scale dependence of this effect. We tested the relationships between stress and disturbance of habitat types and mean local PS for a given trait, using multiple linear regression analysis. A second run was conducted using the inference approach and is presented in Notes S7. Into these analyses we included the following as covariables that might possibly affect mean local PS: mean local species richness and local means of traits (analyses without these covariables are given in Notes S8). We selected variables by best subset search, using adjusted R^2 as the selection criterion (Heinze *et al.*, 2018). We finally tested whether the relationship between disturbance or stress and PS of a given trait changes with scale. For a given trait we characterized each habitat type by its mean local PS and by the PS across its species-pool in the Netherlands, and by mean local species richness and species-pool richness (the latter being an order of magnitude larger than the former, which we compensated for by $\log_e$ transformation of all richnesses). We then related PS to disturbance, stress, species richness, mean-local vs species-pool (1/0), and the interaction terms between local-vs-pool and each disturbance and stress (analyses without species richness are given in Notes S9). Significant interaction terms indicated scale-dependency, and a sign in the same direction as the main effect in the previous analysis indicated that that effect is stronger at the level of local communities than at the level of habitat species-pools. We verified residual normality and homoscedasticity using QQ and predicted-vs-residual plots. Occasionally, it was necessary to exclude residual outliers (see Fig. 4 in the Results section for an example of such an outlier). We report with each analysis the consequence of outlier exclusion. Apart from occasional outliers, residuals always approached normality and homoscedasticity and hence we used a Gaussian error distribution.

Table 2 For seven out of 10 traits phylogenetic signal (PS) within local communities varies more among habitat types than does phylogenetic diversity (PD); that is, *F* values of habitat type are higher.

						Effect on PS > effect on:	
	Effect of habitat type on:	df error	df effect	*F*	*P*	PD?	TD?
	Phylogenetic diversity (PD)	6666	37	60.09	$<10^{-5}$		
Plant height	Trait diversity (TD)	6584	37	270.63	$<10^{-5}$		
	Phylogenetic signal (PS)	6584	37	90.11	$<10^{-5}$	Yes	
Reproduction type	Trait diversity	6428	37	74.03	$<10^{-5}$		
	Phylogenetic signal	6428	37	86.93	$<10^{-5}$	Yes	Yes
Seed shape	Trait diversity	6516	36	277.23	$<10^{-5}$		
	Phylogenetic signal	6516	36	97.72	$<10^{-5}$	Yes	
Seed mass	Trait diversity	6518	37	283.81	$<10^{-5}$		
	Phylogenetic signal	6518	37	53.50	$<10^{-5}$		
SLA	Trait diversity	6597	37	63.14	$<10^{-5}$		
	Phylogenetic signal	6597	37	58.48	$<10^{-5}$		
Breeding type	Trait diversity	6475	37	90.95	$<10^{-5}$		
	Phylogenetic signal	6475	37	62.95	$<10^{-5}$	Yes	
Start/end flowering	Trait diversity	6655	37	175.27	$<10^{-5}$		
	Phylogenetic signal	6655	37	93.78	$<10^{-5}$	Yes	
Flowering duration	Trait diversity	6615	37	129.90	$<10^{-5}$		
	Phylogenetic signal	6615	37	85.60	$<10^{-5}$	Yes	
Life form	Trait diversity	6386	37	338.04	$<10^{-5}$		
	Phylogenetic signal	6386	37	102.21	$<10^{-5}$	Yes	
LDMC	Trait diversity	6564	37	60.63	$<10^{-5}$		
	Phylogenetic signal	6564	37	38.10	$<10^{-5}$		

For one trait, phylogenetic signal varies more among habitat types than does the diversity of the same trait (TD). ANOVAs testing the effect of habitat type on phylogenetic diversity, phylogenetic signal of traits and trait diversities within local communities. See Fig. 2 for an illustration, using reproduction type as an example.

We note that, in our study system, spatial position has little impact on habitat properties as each habitat is characterized by a mean value across spatially distinct local communities spread across much of the region (Notes S10).

Results

PS of traits in local communities differed between habitat types, often more than does phylogenetic diversity of local communities

Mean local PS of the 10 plant traits ranged from very low (0.02) to very high (0.99). Trait diversities of communities ranged from 8.42×10^{-8} to 0.20, and phylogenetic diversities ranged from 36.85 to 204.78 million years ago (Ma). PS, phylogenetic diversity and the diversities of the 10 traits differed significantly between the 38 habitat types (all relationships $P < 0.001$; Table 2; Fig. 2 for the trait 'reproduction type'). ANOVAs (Table 2; Fig. 2) showed that the statistical effect of habitat type on PS was stronger than that on phylogenetic diversity in seven out of 10 traits, and stronger than that on trait diversity for one trait.

Mean local PS within habitat types was very incompletely explained by mean trait and phylogenetic diversities combined

Mean local PSs of six of 10 traits were significantly related to a combination of mean local phylogenetic and trait diversities, with R^2 values ranging from 0.18 to 0.49, with an average of 0.20 (Notes S11; Fig. 2 for the trait 'reproduction type'). However, the fact that residual variation was always more than 51% even in these cases indicates that mean local PS was more than a simple function of trait diversity and phylogenetic diversity.

Habitats with higher disturbance had lower PS

Using the observational approach of ranking habitat environments, we found that mean local PS of all 10 traits decreased with increasing disturbance (Table 3; Fig. 3 for the trait 'reproduction type' as an example and Notes S12 for other traits). Moreover, PS of several traits (reproduction type, SLA, breeding system, flowering date, flowering duration and life form) increased with stress (Table 3; Fig. 3 for the trait 'reproduction type' and Notes S12 for other traits). We note that trait means were significant only in one trait. Mean local PS declined with species richness in eight traits (Table 3). An analysis without trait means and species richness as covariables (Notes S8) confirmed results for disturbance: mean local PS declined with disturbance in 10 traits (Notes S8). Moreover, stress now had a significant and always positive effect on mean local PS in nine traits.

Using the inference approach of ranking habitat environments, we confirmed significant or marginally significant declines of mean local PS with disturbance in six traits, and with species richness in 10 traits (Notes S7). Contrary to the observation approach, we also found significant or marginally significant declines of mean local PS with stress in four traits (Notes S7). The analysis without trait

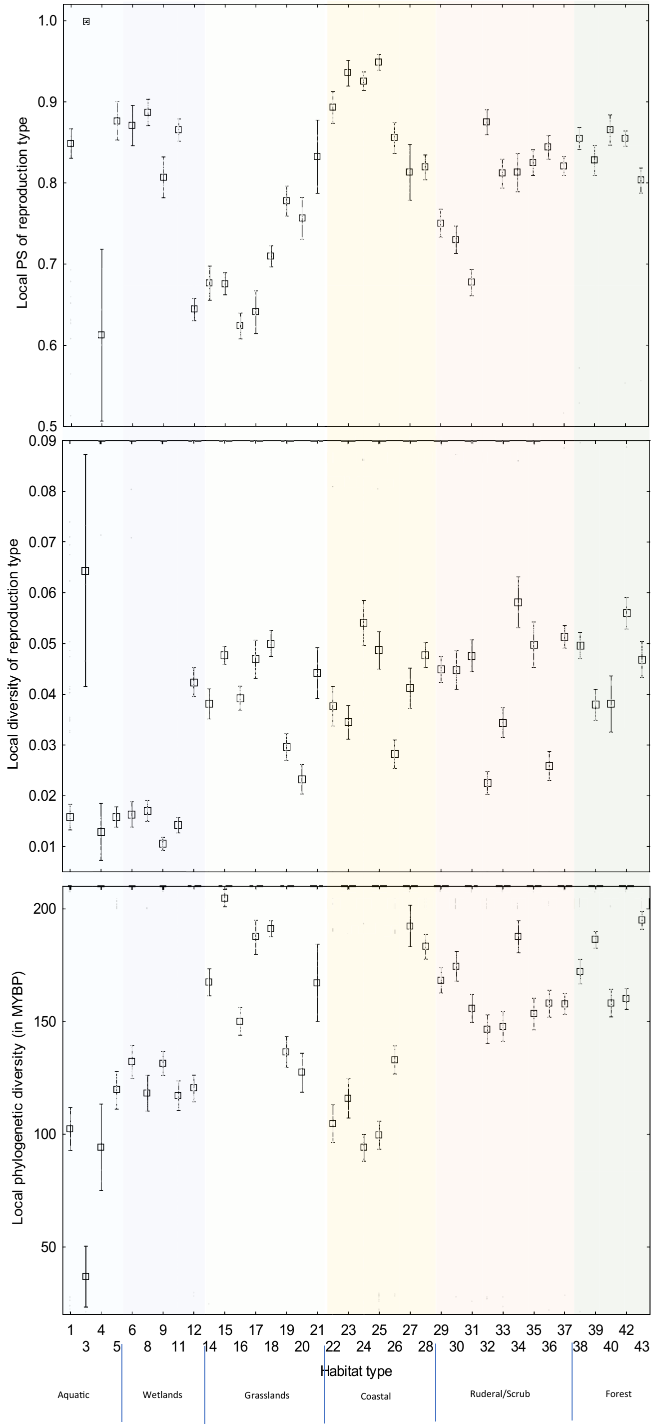


Fig. 2 Habitat types differ in local phylogenetic signal (PS) of reproduction type (top, ANOVA $F_{37,\,6584} = 86.93$, $P < 10^{-5}$). Means and 95% confidence intervals are given. Individual habitat types are identified by numbers (named in Supporting Information Notes S1 Table A) and grouped into major groups (*x*-axis). Also, the diversity of reproduction type and phylogenetic diversity differ among habitat types (middle and bottom; ANOVA $F_{37,\,6584} = 74.03$ and 60.09, respectively; $P < 10^{-5}$). See Table 2 for similar results for all 10 traits. Mean local PS of reproduction type change differently across habitat types than do mean local diversity of reproduction type or mean local phylogenetic diversity. The variation of mean local PS of reproduction type across habitat types can hence only incompletely be explained by a combination of mean local diversity of reproduction type and of mean local phylogenetic diversity ($R^2 = 0.18$; overall similar results for other traits in Notes S11).

means and species richness as covariables (Notes S8) again confirmed results for disturbance: mean local PS declined with disturbance in nine traits, and stress now had a significant and positive effect on mean local PS in two traits.

Mean local PS often related more to stress and disturbance of habitat types than did species-pool PS

Using the observational approach of ranking habitat environments, we found that interaction terms between 'mean-local vs species-pool' and 'disturbance' were significantly or marginally significantly negative in six traits; that is, the above described negative relationship between disturbance and mean local PS was often lost at the level of habitat-species pools (Table 4; Fig. 3 for the trait 'reproduction type' and Notes S12 for other traits). Interaction terms between 'mean-local vs species-pool' and 'stress' were significantly or marginally significantly positive in six traits; that is, the above described positive relationship between stress and mean local PS was often lost at the level of habitat-species pools (Table 4; Fig. 3 for the trait 'reproduction type' and Notes S12 for other traits). However, for stress, two other traits showed the opposite pattern, namely a negative interaction term (Table 4). Note that the main effect of 'mean-local vs species-pool' was nonsignificant in nine out of 10 traits and was $P > 0.1$ in nine traits. Using the inference approach, we found qualitatively similar results: (marginally) significant negative local : disturbance interactions in four traits and (marginally) significant positive local : stress interaction in three traits (Notes S7). 'Mean-local vs species-pool' was nonsignificant in nine traits, and $P > 0.1$ in six traits.

An analysis without species richness as the covariable and using the observational approach confirmed the above results for negative 'disturbance : local' interaction terms in four traits (Notes S9). The stress : local interaction term was now (marginally) significantly positive in eight traits. The main effect of 'mean-local vs species-pool' was now significantly positive in nine traits (although LDMC scores were significantly negative). Using the inference approach, we came to similar conclusions, with local : disturbance interaction terms being significantly negative three times, and local : stress interaction terms being significantly positive three times (but significantly negative for 'plant height').

Overall, for both approaches, mean-local PS declined with habitat disturbance more than species-pool PS, largely independent of species richness. Also, mean local PS was often larger than species-pool PS, and more strongly reinforced by stress than species-pool PS, both of which can be statistically explained by the lower number of species in local communities than across the species-pool. In all above analyses, PS decreased with species richness. This was not due to a numerical sampling effect, as in randomly assembled communities we found no such decrease of PS with species richness (Notes S6).

Table 3 Mean local phylogenetic signal (PS) in a habitat type decreases with disturbance and often increases with stress.

	Disturbance		Stress		Species richness		Trait mean			
PS of trait	t	P	t	P	t	P	t	P	df	Adj R^2
Height	**−5.0552**	**0.0002**			**−3.8887**	**0.0016**			14	0.6465
Type of reproduction	**−5.2264**	**0.0002**	**4.5455**	**0.0005**	**−3.2540**	**0.0063**	1.7053	0.1119	13	0.8470
Seed shape	**−2.9895**	**0.0104**			**−4.9491**	**0.0003**	1.1970	0.2527	13	0.5990
Seed mass	**−4.7282**	**0.0004**			**−4.0936**	**0.0013**	−1.5004	0.1574	13	0.6338
SLA	**−6.0843**	**0.0001**	**2.8431**	**0.0160**	**−3.5531**	**0.0045**	**2.4010**	**0.0352**	11	0.7718
Breeding system	**−4.7128**	**0.0005**	**3.9609**	**0.0019**	**−4.6123**	**0.0006**			12	0.9068
Flowering start end	**−5.8832**	**<0.0001**	*1.8583*	*0.0843*	**4.4986**	**0.0005**			14	0.8309
Flowering duration	**−7.6947**	**<0.0001**	**3.9912**	**0.0018**	**−7.6081**	**<0.0001**	*1.7993*	*0.0972*	12	0.9335
Life form	*−2.0726*	*0.0604*	1.2849	0.2231	*2.0726*	*0.0604*	*−2.0726*	*0.0604*	12	0.6818
LDMC	**−2.6727**	**0.0182**	*2.0065*	*0.0645*					14	0.2673

These relationships are illustrated for type of reproduction in the left part of Fig. 3. Significant ($P < 0.05$) relationships to disturbance or stress are indicated in bold, and marginally significant ($0.05 \leq P < 0.1$) in italics. Species richness and mean trait values are included as covariables. Variables have been selected by a best subset search, using adjusted R^2 as a criterion. Disturbance and stress are ranked by observational approach (see Supporting Information Notes S7 for inference approach). A maximum of two residual outliers were excluded, not changing the conclusions on the effect of disturbance, but rendering the effect of stress (marginally) significant in three cases and nonsignificant in one case. Analyses without covariables species richness and trait mean are given in Notes S8 and tend to confirm a negative relationship of PS to disturbance and an often positive relationship to stress.

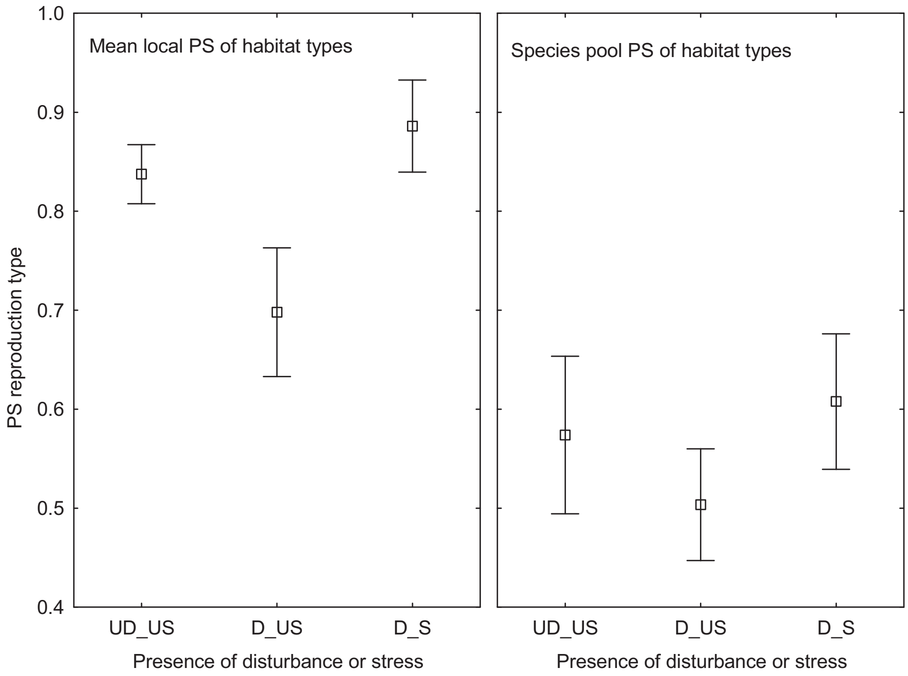


Fig. 3 Relationship between disturbance regime (UD, undisturbed vs D, disturbed) or stress regime (US, unstressed vs S, stressed) of habitat types and the phylogenetic signal (PS) of 'reproduction type'. PS is quantified either within local communities and the mean is calculated within each habitat type (left) or across the entire species-pool of each habitat type within the study region (right); $n = 18$ habitat types. Per category of habitat types, means and 95% confidence limits are given. Mean local PS of reproduction type in a habitat type (left) tends to decrease with disturbance ('D' vs 'UD') and to increase with stress ('S' to 'US') ($P < 0.001$, Table 3). At the level of habitat species-pools (right) these relationships to disturbance and stress tend to disappear (corresponding to significant interaction terms of either disturbance or stress with 'mean local' in Table 4). Table 3 shows similar relationships of mean local PS to disturbance and stress, and Table 4 similar scale-dependency, for most to all other traits. Disturbance and stress regime were ranked based on observations, namely names of habitat types, representing three of the possible combinations of stress and disturbance. See Notes S7 and S9 for analyses using continuous gradients of stress and disturbance inferred from species ranks in disturbance and stress tolerance.

Mean local PS was only sometimes correlated with PS in the corresponding habitat species-pools, contrary to phylogenetic and trait diversities

For six out of 10 traits, mean PS of local communities per habitat type was significantly positively correlated with the PS of the corresponding habitat species-pools (Table 5; Fig. 4 for the trait 'reproduction type'). By contrast, mean diversities of traits of local communities per habitat type were significantly positively correlated with the trait diversity of the corresponding habitat species-pools in all but one trait (LDMC), and the same correlation was observed for phylogenetic diversity (Table 5). Local/

Table 4 The relationship between habitat disturbance and PS becomes at least marginally significantly more negative when PS is quantified as the mean across local communities in a habitat type than when quantified across the habitat species-pool, contributing to the negative overall relationship (shown in Table 3) in six traits.

	Mean local (vs species-pool)		Disturbance		Stress		Log$_e$ no. of species		Mean local: disturbance		Mean local: stress			
PS of trait	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	df	Adj R^2
Height	−0.9724	0.3389	−1.1012	0.2799	−2.0485	0.0497	−2.3734	0.0245	**−4.1737**	**0.0002**	**3.5451**	**0.0014**	29	0.4678
Type of reproduction	−0.0801	0.9367	−5.1963	0.0000	3.2754	0.0028	−4.9019	0.0000	*−1.7021*	*0.0998*	*2.0336*	*0.0516*	28	0.9259
Seed shape	−1.1600	0.2562	−3.3486	0.0024	−2.9461	0.0066	−4.8637	0.0000	*−1.7625*	*0.0893*	**5.9590**	**0.0000**	27	0.8578
Seed mass	−2.1872	0.0376	−0.1372	0.8919	−2.5327	0.0174	−3.2629	0.0030	**−3.1460**	**0.0040**	**2.4569**	**0.0207**	27	0.3772
SLA	0.8799	0.3862	−6.0705	0.0000	2.7952	0.0091	−1.6117	0.1179	1.5789	0.1252	*−1.7585*	*0.0892*	29	0.8379
Breeding system	−1.6832	0.1035	−2.5281	0.0174	0.2112	0.8343	−5.6094	0.0000	−0.3789	0.7077	0.0591	0.9533	28	0.8928
Flowering start end	1.0528	0.3018	−8.6671	0.0000	3.0424	0.0052	−5.0320	0.0000	**−2.9102**	**0.0072**	**2.3716**	**0.0251**	27	0.9546
Flowering duration	−1.0009	0.3255	−5.8704	0.0000	0.8223	0.4179	−7.6384	0.0000	**−3.0609**	**0.0048**	**2.6443**	**0.0133**	28	0.9544
Life form	−0.4175	0.6794	−5.1667	0.0000	−0.2000	0.8429	−3.1200	0.0041	−0.9289	0.3606	1.6492	0.1099	29	0.7957
LDMC	0.2777	0.7833	−4.0039	0.0004	2.4733	0.0197	−2.6934	0.0118	1.0777	0.2904	**−3.1638**	**0.0037**	28	0.8682

The relationship between habitat stress and PS becomes at least marginally significantly more positive, contributing to the positive overall relationship (shown in Table 3) in six traits (albeit two traits show the opposite pattern). Disturbance and stress are ranked according to the observational approach (see Supporting Information Notes S7 for relationships with disturbance and stress quantified according to the inference approach). These relationships are illustrated for 'type of reproduction' in Fig. 3, left vs right part. Significant ($P < 0.05$) interaction terms are indicated in bold, and marginally significant ($0.05 \leq P < 0.1$) in italics. Species richness is included as a covariable (log$_e$ transformed as pool-richness tend to be orders of magnitude larger than local richness). See Notes S9 for an analysis without species richness. A maximum of two residual outliers were excluded, contributing to the (marginal) significance of four interaction terms for both disturbance and stress.

species-pool correlations were weaker for PS than for trait diversity in eight out of 10 traits, and weaker for PS than for phylogenetic diversity in five traits (Table 5).

Discussion

We found that local PS of each trait shows highly significant variation among habitat types, more than phylogenetic diversity. In some traits, means of local PS within habitat types related positively to PS of the corresponding species-pools, but relationships were usually weaker than for trait and phylogenetic diversities. Moreover, local PS of traits was far from being a mere function of phylogenetic and trait diversities. Remarkably, local PS of all traits decreased with habitat disturbance – and it did so more strongly compared with the PS of the habitat species-pools. These results were consistent across two approaches of ranking habitats as being disturbed (by contrast to the results on relationships of PS to stress, which were weaker and inconsistent across approaches, which we hence refrain from interpreting). We recall that the observed patterns cannot be explained by the presence of exotics (see the Materials and Methods section), nor by possible stochasticity within small, species-poor samples (species richness was always accounted for, and patterns of PS were strongest locally, despite smaller richness values).

Local plant communities in a given habitat might theoretically maintain strong local PS of traits, high phylogenetic or high trait diversity without any contribution of present local processes, but solely due to a random sampling of species from the corresponding habitat species-pools that have evolved under the particular environmental constraints that characterize each habitat type (Fig. 1, scenario 2; Table 1 H5–8; Mittelbach & Schemske, 2015). If that is the case, we should expect to find a strong positive correlation between mean local PS of habitat types and the PS of the species-pools of the same habitat types. While such a positive correlation between mean local and species-pool was indeed observed for diversities of most traits, and for phylogenetic diversity, it was absent for PS of four out of 10 traits and was often only moderate for the remaining six. Moreover, the decline of PS with disturbance was often stronger for mean local PS of habitats than for species-pool PS of habitats. This result implies that the extent to which traits within local communities reflect phylogenetic position cannot be solely explained by the macroevolution of species-pools under particular habitat constraints. Rather, local assembly processes remain important. If this local assembly occurs under undisturbed habitat conditions, PS increases.

Also, local plant communities in a given habitat type could maintain strong local PS solely as a result of a particular combination of phylogenetic and trait diversity, such as a low trait diversity with constant phylogenetic diversity (Weiher *et al.*, 2011; Gerhold *et al.*, 2015). However, our results show that variation of mean local PS across habitat types is only partly explained by phylogenetic or trait diversity. Moreover, we found that phylogenetic and trait diversities within local communities of a habitat type depend more strongly on the composition of the habitat species-pool than does local PS. Consistently, relationships of PS to habitat disturbance or stress emerged locally rather than across the pools. These observations suggest that a given environment can locally maintain the outcome of a specific

Table 5 Mean local phylogenetic signal (PS) of a trait in different habitat types only incompletely mirrors the PS of the same trait in the species-pools of habitat types.

	R^2 PD	R^2 PS	R^2 TD	R^2 PS < R^2 PD?	R^2 PS < R^2 TD?
Phylogenetic diversity	**0.2300**				
Plant height		**0.1541**	**0.7401**	Yes	Yes
Reproduction type		**0.4868**	**0.2059**		
Seed shape		0.0716	**0.5968**	Yes	Yes
Seed mass		0.0059	**0.3743**	Yes	Yes
SLA		**0.3135**	**0.4018**		Yes
Breeding type		**0.3771**	**0.3900**		Yes
Start/end flowering		**0.2813**	**0.6561**		Yes
Flowering duration		0.0723	**0.2413**	Yes	Yes
Life form		**0.4712**	**0.7441**		Yes
LDMC		0.0511	0.0222	Yes	

Relationships are weaker than for mean local phylogenetic diversity (PD) in five out of 10 traits, or for mean local diversity (TD) in eight out of 10 traits. Explained variances from simple Pearson correlations; significant relationships ($P < 0.05$) are indicated in bold (> 0.1 for the remaining relationships); $n = 38$ (37 for PS of seed shape). Up to one residual outlier was excluded for PS (rendering one pool vs local relationship significant) and up to two for trait diversity (not changing significances). See Fig. 4 for an illustration using PS of reproduction type.

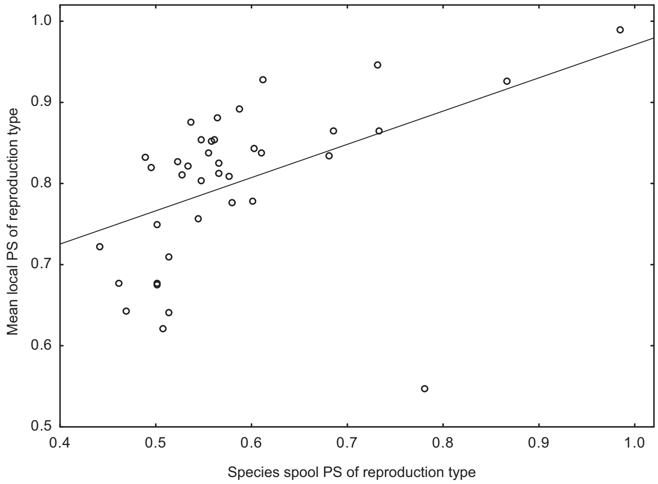


Fig. 4 Phylogenetic signal (PS) of reproduction type within local communities of habitat types is only partly related to PS within the species-pool of the same habitat types across the region ($R^2 = 0.22$, without outlier: 0.49), suggesting that a major part of the variation among habitat types in local PS is determined by local processes. See Table 5 for overall similar results for PS of other traits.

scenario of trait evolution, not just particular levels of diversity. Local PS is therefore a unique characteristic of habitat types.

The strong responses of local PS to the environmental gradients can be interpreted in the light of the scenarios of assembly and selection outlined in the Introduction (Table 1; example in Fig. 1, scenario 1). Along the disturbance gradient, we observed a decrease in local PS. Decreases in local PS in particular habitat types may reflect two scenarios: increasing differences among close relatives or decreasing differences among distant relatives, with the former resulting in low phylogenetic and high trait diversities (Prinzing *et al.*, 2017), and the latter in the inverse. The scenario of decreasing functional differences among distant relatives may be more strongly supported given that, overall, PS tends to decrease with an increase in phylogenetic diversity and a decrease in trait diversity (Notes S11). However, given that phylogenetic and trait diversity only very incompletely explain local PS, both scenarios are probably occurring simultaneously in different disturbed habitat types, perhaps reflecting the fact that disturbance events may take multiple forms with abiotic or biotic origin. Disturbances commonly create environmental heterogeneity because of the intrinsic variation in shape, size and severity of the disturbance events (Grime, 2006; Turner, 2010; Ponge, 2013). Disturbances also create fluctuating environments and thereby may favour stabilizing niche differences (contributing to the 'storage effects', Chesson, 2000), permitting functionally diverse species to coexist (Table 1, H3). This diversity may include both functionally diverse close relatives or distant relatives convergent on one functional trait (but probably divergent on other, more conserved traits). Finally, disturbances should have proportionally greater effects on abundant and dominant species, allowing inferior species with lower competitiveness to profit proportionally most strongly from available resources (Chesson, 2000), and these inferior species may be functionally or phylogenetically more diverse than the dominant species. Overall, spatiotemporal fluctuation of environmental conditions or competition-free space may allow, within lineages, the species with diverging trait values to establish, thus reducing local PS in traits. Establishment of diverging trait values in disturbed sites may explain why similar 'ruderal' strategies have originated within different lineages, while strategies of responding to stress or competition may have been more strongly conserved (as suggested by Grime, 2006).

We considered a wide range of traits, some of which are important for the niche position and survival of adults (flowering start/end, LDMC, SLA, life form) and their competitive dominance (height, flowering duration), for movement and survival of seeds/seedlings (seed mass, seed shape), or for ensuring reproduction (reproduction type, breeding system) (Pérez-Harguindeguy *et al.*, 2013). However, traits of a given group rarely showed the same relationships to disturbance or stress. Disturbance, for instance, related to a significant decrease in PS in all traits except LDMC. We do see one case where traits of a given group seemed to show similar patterns: PS of both reproduction type and breeding system increased under stress when measured by the observation approach (with or without covariables) or the inference approach (without covariables). Possibly, stress selects for specific ways of ensuring reproduction mastered by specific lineages, while without stress reproduction may be less difficult to ensure. By contrast, traits related to survival and competitiveness may be filtered within lineages by both abiotic stresses and competitive hierarchies in stress-poor habitats (Kunstler *et al.*, 2012), leaving no signal of stress. Also, traits of a given group rarely showed the same relationships of PS to mean values of traits. Means of species traits were significant in only one trait in the observational approach (four in the inference approach, Table 3; Notes S7). An individual trait probably does not capture stress or disturbance as efficiently as either of the two measures of stress or disturbance that we included in the same models. Moreover, trait means might also be related to PS in ways other than being an (incomplete) proxy of the environment. For instance, some life forms have been suggested to be particularly evolutionary difficult to acquire or to lose (Scheffer *et al.*, 2014), which should increase PS. These multiple and incomplete relationships of trait means to trait PS might cancel each other out. Finally, trait means might relate to PS through a random sampling effect, but we find that this is hardly the case (Notes S13).

We found that PS tended to be higher at the level of means across local communities within habitat types than at the level of habitat species-pools, and could statistically explain this effect by the lower number of species within local communities compared to species-pools. The observed increase of PS with decreasing species richness might be due to biological processes or to numerical sampling. If it is numerical sampling, a null model with random sampling of decreasing numbers of species should reproduce the observed increase of PS with declining species richness. It does not (Notes S6), suggesting that biological processes are responsible for the observed increase of PS with declining species richness. One such biological process might be that related species may more easily coexist if they differ in traits (Dayan & Simberloff, 2005; Prinzing *et al.*, 2008). Increasing numbers of related species, and thereby overall species richness, hence would require decreasing PS.

Overall, while our evolutionary explanations of patterns of local PS remain speculative and open to criticism (Revell *et al.*, 2008; Kaliontzopoulou & Adams, 2016), our results clearly show that, locally, strong PS is not the rule, contrary to assessments across entire clades or regional biota (Peterson, 2011). Local PS depends on habitat characteristics and should be assessed rather than taken for granted. Specifically, our results suggest that local assembly processes in disturbed habitats allow the establishment of related plant species with diverging trait values or unrelated species with converging trait values. In disturbed habitats, deep-past, interspecific evolution relates little to present trait values. This result may have implications for the interpretation of community phylogenetic patterns: in disturbed habitats, these patterns may reveal only little about the trait composition of communities, or any supposedly evolutionary drivers of community assembly. Inversely, undisturbed habitats might defy the widespread vision that past macroevolutionary patterns emerge at the level of entire regions and become locally overlaid by dispersal and species interactions (Ricklefs, 2008; Guisan & Rahbek, 2011; but see Prizing *et al.*, 2016). In undisturbed habitats the opposite is true: the signal of macroevolution in trait states is much larger locally than across the species-pool, probably reflecting reduced species richness locally. This result may also have implications for conservation: communities in disturbed environments might have a conservation value as they maintain the exceptional species within lineages, the species with trait values diverging from the other lineage members and converging with trait states of other lineages. This conservation value of disturbed habitat types would pass unnoticed when only looking at local phylogenetic diversity (being insignificantly smaller in disturbed habitat types; results not shown). We are not aware of any systematic treatment of PS as a conservation criterion in the literature, and so it remains unknown whether habitats of low PS are particularly threatened (equivalent to tests in Bartish *et al.*, 2020). Interestingly, at the global scale, some regions of highest conservation concern are emblematic for maintaining species of particularly diverging trait states within lineage (e.g. the Galapagos archipelago with diverging beak traits in Darwin finches) or for particularly converging trait states between lineages (e.g. polar waters with converging adaptations for swimming in 'fish', mammals and birds). Finally, if ancestry is only little related to trait values of plant species, ancestry might also not be related to interactions of plants with herbivores and mutualists, permitting lineages of herbivores or mutualists to establish on new lineages of plant hosts.

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Author contributions

AP, BY, CV, DSM, EW, HJ, IVB, IK, JH, MB, MRH, MW, OP, SP and WO designed the concept. SH and WO managed and provided the Dutch plant community data. IB estimated the phylogeny. BY cleaned and assembled the trait, community and phylogenetic dataset. SP, AP and BY designed the analyses. BY, AP and SP performed all the analyses. All authors discussed the results. AP and BY wrote the first draft of the manuscript, to which CV, DSM, EW, HJ, IVB, IK, JH, MB, MRH, MW, OP, PV, SH, SP and WO contributed critically and gave final approval for publication. AP and BY contributed equally to this work.

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Data availability

The dataset containing the composition of the plant communities of the Netherlands, the trait data and the phylogeny reconstructed by Igor Bartish are available via the SynBioSys database, the BIOFLOR database (www.ufz.de/biolflor) and TreeBase (ID: S13572), respectively. The measure of phylogenetic signal, functional and phylogenetic diversities, and S and R values averaged by habitat types (i.e. the final data presented) is deposited in Dryad (https://doi.org/10.5061/dryad.dv41ns201).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Criteria for retaining local communities, sample sizes of communities and species, calculation of phylogenetic signal and baseline data per habitat type.

Notes S2 Ranking of habitat types for local disturbance and stress.

Notes S3 Definitions of species traits.

Notes S4 Sufficient resolution of our phylogenetic tree.

Notes S5 Relationship between the standard deviation of phylogenetic signal (PS) and species richness.

Notes S6 Effect of species richness on local PS in randomly sampled communities.

Notes S7 Relationship of mean local PS to habitat disturbance and stress using the inference approach, accounting for covariables.

Notes S8 Relationship of mean local PS to habitat disturbance and stress using the observational approach and inference approach, without accounting for covariables.

Notes S9 Relationship of mean local PS to disturbance, stress and their interaction with local (vs species-pool), without accounting for species richness.

Notes S10 Distributions of habitat types across the Netherlands.

Notes S11 Relating mean local phylogenetic signal to mean local trait and phylogenetic diversities.

Notes S12 Relationship between disturbance or stress regime of habitat types and the phylogenetic signal (PS) of traits.

Notes S13 Effect of trait means on trait phylogenetic signal (PS) in randomly sampled communities.