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Different habitats within a region contain evolutionary heritage from different epochs depending on the abiotic environment

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Running title: Habitats contain evolutionary heritage from different epochs

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Abstract:

Aim Biodiversity hot-spots are regions containing evolutionary heritage from ancient or recent geological epochs, i.e. evolutionary ‘museums’ or ‘cradles’, respectively. We hypothesize (i) there are ‘museums’ and ‘cradles’ also within regions: some species pools of particular habitat types contain angiosperm (flowering plants) lineages from ancient geological epochs, others from recent epochs; (ii) habitat-specific abiotic factors control numbers of angiosperm lineages contained from a given epoch in a given habitat species pool.

Location The flora of the Netherlands

Methods We studied the world’s largest vegetation-plot database and a new, uniquely resolved dated angiosperm phylogeny available for the Netherlands. We characterized species pools of habitat types by a novel concept: epoch-specific lineage diversities.

Results We found that species pools of most habitat types were characterized by over- or underrepresentation of lineages from at least one epoch, dating back until the origin of angiosperms. These patterns are not captured by mean lineage ages. Abiotic environments explained on average 56% and up to 75% of the variance in numbers of lineages per epoch, but with opposing effects of the same factor for different epochs. Specifically, warm and dry habitats tend to contain lineages dating back to warm and dry epochs. Identifying lineages from sets of random time intervals rather than from a set of geological epochs significantly reduced relationships with the environment.

Main conclusions Within a region, habitat types differ significantly in the evolutionary heritage they contain from different geological epochs, and the environment controls these differences.

Key words: epoch-specific net diversification, dated phylogeny, macroevolutionary ecology, museums and cradles of diversity, paleoecology

INTRODUCTION

Life has passed through different geological time periods (epochs) of very different dominant environments. Lineages (continuous lines of descent of species) that diversified during a particular epoch might be particularly adapted to live under the environmental conditions dominant during that epoch. An obvious example is found in lineages of succulent plants that diversified in epochs of increased aridity (Arakaki *et al.*, 2011). Today in the expanding desert environments succulents are more apt to survive and more abundant than, for instance ferns or lycophytes, that mostly diversified in epochs dominated by moister environments (DiMichele *et al.*, 2004).

Following Stebbins' (Stebbins, 1974) metaphor, it has been suggested that floras in certain regions may function as 'museums' of diversification of biota, containing lineages from ancient epochs, or as 'cradles' containing lineages from recent epochs. These regions are characterised respectively by a high number of either ancient or recent lineages (Hawkins *et al.*, 2006). Such phylogenetic age structures of floras and faunas from these regions depict strong increments of the diversity of (sub) lineages that date back to the beginning or the end of the time axis, respectively. Recently, some regions were suggested to function as 'hot-spots' serving both as museums and cradles of biodiversity (McKenna & Farrell, 2006; Lopez-Pujol *et al.*, 2011).

Similarly to species pools of different regions, species pools of different biomes and habitat types within a region, i.e. species present across all patches of that biome/habitat, might vary in the identity of phylogenetic lineages they represent (Prinzing *et al.*, 2001; Crisp *et al.*, 2009; Bartish *et al.*, 2010; Kozak & Wiens, 2010). We demonstrate in supplementary on-line

material Appendix S1 that differences in lineage composition among species pools of habitat types of angiosperms (flowering plants) might well exist even within a relatively small and geologically young region under strong impact of recent anthropogenic environmental changes (see also Bartish *et al.*, 2010). Specifically, (i) different habitats within a given region may in many respects represent a similarly wide range of environments as different regions; (ii) species often use similar habitats on different continents; (iii) lineages rarely shift habitats ('phylogenetic signal'); (iv) stochastic or transient ecological factors that may control the composition of local patches of habitat types might average out at the scale considered here, i.e. the entire species pools of habitat types across all local patches.

However, it has never been studied whether habitat types differ in the phylogenetic age structures of the species pools they contain. For instance, do within a given region some habitat types serve as 'museums' by containing lineages that date back to earliest geological epochs, while others serve as 'cradles' containing youngest lineages? We hypothesize that this is the case. Specifically, we predict that within a given region, angiosperm lineages from a given geological epoch are overrepresented in the species pools of some habitat types and underrepresented in others. We predict also that within a given habitat type lineages from some geological epochs are overrepresented, while lineages from the other epochs are underrepresented. We stress that a habitat type within a region containing a large number of lineages from a given epoch does not equal lineages during that epoch originating in that habitat type. However, it does mean that today within this region this habitat type serves a function in maintaining the lineages from that epoch.

The presence of 'museums' or 'cradles' at the regional scale has usually been explained by their environment, such as temperature and moisture, or more generally latitude (Hawkins *et al.*, 2006, Svenning *et al.*, 2008). Specific environments, such as high temperature and

moisture in the tropics, have been suggested to either decrease extinction in the case of ‘museum’ environments (Hawkins *et al.*, 2006; Kissling *et al.*, 2012; Rolland *et al.*, 2014), or increase speciation in the case of ‘cradle’ environments (Weir & Schluter, 2007; Jansson & Davies, 2008; Rolland *et al.*, 2014). However, a region might also be a ‘museum’ (or ‘cradle’) because it represents an environment in which lineages from one particularly early (or recent) epoch have originated or survived. For instance, in the above example of succulent lineages their present occurrence in dry regions may correspond to origin and survival during particularly dry epochs. Dry regions hence maintain high diversity of lineages from these but not from other epochs. Here we hypothesize that also within a region differences in ‘cradle’/‘museum’ nature of habitat types reflect differences in the abiotic environments in these habitats. More specifically, we hypothesize that the same abiotic environment, such as low soil moisture, can have a positive effect on numbers of lineages a habitat type contains from some epochs, but no effect or a negative effect on numbers of lineages contained from other epochs.

A useful test of our hypotheses can only be achieved by studying a major and phylogenetically well analysed taxon across a region of diverse habitat types being well characterised in terms of species pools. We used the currently world’s largest vegetation-plot database (Schaminée *et al.*, 2012) characterising a region with a high diversity of habitat types under major human impacts, i.e. the Netherlands. To test our above predictions we pooled species compositions from local habitat patches into regional species pools for different types of habitats and then quantified for each species pool the diversity of angiosperm lineages dating back to different geological epochs. We tested the relationships between abiotic characteristics of habitats and lineage diversities from the different geological epochs and from random sets of time intervals.

METHODS

Defining and characterizing habitat types

The Dutch National Vegetation Database is currently the largest database of its kind in the world, covering the whole range of vegetation types in the country (Schaminée *et al.*, 2012; <http://www.synbiosys.alterra.nl>). The database is registered in the Global Index of Vegetation-Plot Databases (<http://www.givd.info/>; ID: EU-NL-001), from which the metadata are available. The database we used contains records of 1,283 currently accepted species of angiosperms in the region after exclusion of hybrid species and subspecies from the total list of Dutch angiosperms. Exotic species were also excluded to avoid distortions of phylogenetic structure by representatives of geographically distant and evolutionarily very different floras (exotics are those that colonized the region after 1500 AD, a list can be found at <http://www.milieuennatuurcompendium.nl/tabellen/nl139802a.html>, they account for 16% of the total sample of species). We referenced names against the checklist of the Integrated Taxonomic Information System: <http://www.itis.gov/>).

In the Dutch vegetation database, vegetation types have been hierarchically classified based on cluster analyses of species compositions of vegetation plots, a powerful way of objectively identifying habitats for plants within a region (Schaminée *et al.*, 1995-1999), and independent of any phylogenetic relationships among species. The classification covers all plant habitats (including major gradients in light and nutrient availability, moisture and soil

reaction) given that vegetation scientists have purposefully studied even the rarest habitats within the region rather than only the abundant ‘typically Dutch’ habitats. Specifically, we considered the level of vegetation classes, with 43 classes providing an informative but still manageable resolution of the entire spectrum of habitats representing all ecological and environmental conditions for this region. (Note that the much used habitat classification of Natura-2000 European habitat directive identifies only particularly rare habitats; these rare European Natura-2000 habitat types can be cross-linked to the complete Dutch habitat typology we used.) We used a stratified-by-habitat selection of 36,328 plots available from Turboveg (Hennekens & Schaminée, 2001). We defined the species pool of a habitat type as all species in all plots belonging to a particular habitat type following Bartish *et al.* (2010). Justification of this approach for regional species pools has been developed in Zobel (1992). See also Lessard *et al.* (2012) and Cornell & Harrison (2014) for recent overviews of the species pool concepts.

We also characterized each habitat type by its ground water level, light, soil reaction, soil phosphorus, and temperature conditions. As measuring abiotic environment in each plot is infeasible, we used species indicator values to infer environmental conditions, averaged across species in plots within habitats. Species indicator values have been shown to permit reliable inferences on the environmental conditions at a locality (Ertsen *et al.*, 1998; Hennekens & Schaminée, 2001; Wamelink *et al.*, 2002). For details of estimation of species indicator values see Appendix S2. The database used in our analyses has been registered in the Global Index of Vegetation-Plot Databases (ID: EU-00-006). We finally quantified for each habitat type the total surface of plots sampled. Specific values per habitat type are reported in Appendix S2.

Estimation of mean lineage ages of species pools of habitat types

We used the dated tree of all 1,283 Dutch angiosperm species (excluding hybrids, subspecies, and exotics) available from TreeBase ID: S13572, resolved at genus level or finer (Hermant *et al.*, 2012) and polytomies were further resolved by phylogenetic analysis for some old genera, as explained in Appendix S3. The following analyses were conducted based on this tree. This tree still contained some polytomies and we explored their possible impact on the results by creating 100 randomly resolved trees (see Appendix S3 for details) and calculating the different dependent variables for each of these trees and correspondingly redoing the analyses 100 times. We constructed dated phylogenies for each habitat species pool and then calculated Mean Phylogenetic Distance between pairs of species in the pool using calculation in Phylocom 4.1 (Webb *et al.*, 2008). Observed Mean Lineage Ages (*MLA*, which is Mean Phylogenetic Distance, divided by 2) of a given habitat species pool were standardized by a null expectation ('Phylogeny shuffle' in Phylocom 4.1) created by randomly sampling 999 times the same number of terminals from the tree of all species in the sample as: (observed age – mean null-expected age) / standard deviation of null expected age. We note that application of other null expectations available in Phylocom 4.1 resulted in similar values of our standardized parameters (results are not shown). All further analyses were based on such standardized Mean Lineage Ages (*stMLA*). We also estimated the significance of the observed mean lineage ages by determining their percentile position within the null expectation. In addition, we calculated *stMLAs* per habitat type for each of the 100 randomly resolved trees and then averaged these values within habitat types.

We note that we also explored the use of Faith's Phylogenetic Diversity PD (Faith, 1992), calculated using 'pd' command in Phylocom 4.1. PD was related to roughly similar present environments as *stMLA* (notably phosphorus), but much less so ($R^2=0.03$), and PD required

accounting for species richness as co-variable (e.g. Davies *et al.*, 2007). PD was hence not considered.

Lineages-through-time plots

Age structure within phylogenetic trees can be summarized as Lineages-Through-Time (LTT) plots. \log_2 -transformed numbers of lineages (branches) from a tree are calculated for specified age intervals and plotted against mean ages of these intervals. We did so for sub-trees of the tree of regional species pool, each sub-tree was representing only the species present in particular habitat species pool. We reconstructed LTT plots for all 43 habitat species pools (Appendix S4) using LTTR module of Phylocom 4.1 (Webb *et al.*, 2008). This module permits specifying the width of age intervals across a given dated tree and any sub-tree, generated from this tree by Phylocom 4.1.

Diversities of lineages of Dutch angiosperms dating back to a given epoch and contained by different habitat types

We again used the sub-trees per habitat type and selected time intervals for estimation of lineage diversities, accounting for existing knowledge about ages of geological epochs. We used ages of geological epochs from geological time scale (Walker & Geissman, 2012) and pooled or split some of these epochs where paleoclimatic reconstructions suggested similarity between or major difference within geological epochs (Zachos *et al.*, 2001; Dupont-Nivet *et al.*, 2007). We hence selected the following seven epochs: from the age of the crown node of the total tree of regional flora (164 Ma) to 126 Ma, which corresponds to diversification of

angiosperms from the Late Jurassic until the middle of the Early Cretaceous; 126 Ma – 100 Ma, which corresponds to the Barremian/Aptian Ages boundary until the end of the Early Cretaceous; 100 Ma – 66 Ma (the Late Cretaceous); 66 Ma – 33.9 Ma (the Paleocene and the Eocene); 33.9 Ma – 23 Ma (the Oligocene); 23 Ma – 5.3 Ma (the Miocene); 5.3 Ma – present (the Pliocene, the Pleistocene, and the Holocene). We supplemented these analyses based on seven geological epochs and their paleoenvironments by analyses of time intervals between 164 Ma and present, defined independently of geological epochs: (i) as 100 sets of seven random time intervals; (ii) as seven equal-sized time intervals (i.e. 24.3 Ma).

For each epoch and each habitat type we calculated Epoch-specific Lineage Diversities (ELDs), defined as diversity of lineages dating back to a given geological epoch within a given habitat species pool. The index measures the proportional increase in numbers of lineages-through-time, i.e. \log_2 numbers of phylogenetic branches dating back to a given epoch (\log_2 number of branches at the end of the epoch minus \log_2 numbers of branches at the end of the preceding epoch).

We standardized our estimates of ELDs by null-expectations for species pools of given sizes from a regional species pool. Null-expectations ('Phylogeny shuffle' option in Phylocom 4.1) of ELDs were computed for all species pools and all age intervals as means across 999 random samples of a given number of species from the total tree of Dutch Angiosperms. We performed these calculations using a modified version of LTTR module of Phylocom 4.1 (the code is available from MIB and will be implemented in one of further versions of Phylocom). For each time interval in each habitat species pool we calculated differences between observed and means of null-expected ELDs, divided by standard deviation of the null-expected ELDs. All analyses presented in the Results were based on such standardized, unbiased *stELD* values. We also estimated the significance of the observed ELDs for each

time interval and habitat type by determining their percentile position within the null expectation. We note that, despite being standardized for species richness, high *stELDs* for a given epoch in general correspond to high present species richness (simultaneously accounting for all epochs and surface sampled, and excluding two outliers, results not shown). This observation further suggests that *stELDs* are informative about historical footprints in present diversity. We finally calculated *stELDs* per habitat type and epoch for each of the 100 randomly resolved trees and then averaged these values within epochs per habitat type.

Relating phylogenetic structures to the abiotic environment within habitat types

We analyzed the effects of abiotic environmental characteristics of habitat types on *stMLA* of the corresponding species pools. We applied multiple linear regression using as predictive variables all five environmental variables simultaneously (STATISTICA version 8; Statsoft Inc. Maisons-Alfort, France). *Surface area* per habitat type was used as a co-variable in all multiple regression analyses to control for possible sample size bias (Rosenzweig, 1995; Bartish *et al.*, 2010). We graphically verified the assumptions of the analyses on residual distributions using predicted vs. residual and normal probability plots and found that residual distributions approached homogeneity and normality. In order to reduce multi-collinearity among predictive variables we conducted a best-subset search, using adjusted R^2 as a search criterion. Adjusted R^2 resembles the Akaike or Mallow criteria but has a goal to maximize the explained variance while accounting for the remaining degrees of freedom, not to identify a minimum set of predictor variables. We then repeated this approach and analyzed effects of abiotic characteristics of habitats on their *stELDs* from a given epoch. In other words, we

identified how present abiotic characteristics of habitats affect the function of the corresponding habitat species pools in maintaining the diversities of lineages dating back to the given epoch. We repeated this analysis for each epoch. To summarize how much variance of *stELDs* can be explained by abiotic environments, we averaged the R^2 values from all seven epochs. We compared this to averages of the R^2 calculated (i) across each set of seven random time intervals, and (ii) across the seven equal sized time intervals.

RESULTS

We found that unstandardized mean lineage ages (*MLA*) vary among habitat species pools between 111 Ma and 131 Ma (Fig. 1(a), unstandardized values). This relatively small range might correspond to strong representation of both monocots and core-eudicots (the two most speciose clades of angiosperms) in all habitat types. Despite this relatively small range, many of the standardized *MLA* (*stMLA*) deviate from what would be expected by random for a given species richness. In most habitats, *stMLA* are significantly younger than expected from random distribution of *MLA* for a given species richness, notably in ‘Bramble underscrub of woodland edges and clearings’ (Fig. 1(a), standardized values, habitat type 35). In some habitat species pools *stMLA* are significantly older than expected by random, notably in ‘Free floating Duckweeds’ and ‘Floating or submerged rooted plants in fresh waters’ (Fig. 1(a), habitat types 1 and 5). We also found that randomly resolving the trees yielded *stMLAs* (averaged across all 100 randomly resolved trees) that were nearly identical to those of the non-resolved trees ($r^2 = 0.999$, see Appendix S5 for raw values). Polytomies hence did not introduce a bias.

In multiple regression analysis *stMLAs* of habitat species pools were strongly related with the abiotic characteristics of these habitat types ($R=0.86$, $F=26.98$, $P<0.001$). High *stMLA* of habitat types corresponded to high ground water level ($t=5.30$, $P<0.001$), high phosphorus availability ($t=3.88$, $P<0.001$), low soil pH ($t=-2.40$, $P=0.021$) and low temperature (which however was non-significant at $t=-1.01$, $P=0.317$).

The standardized diversities of lineages dating back to a particular epoch (*stELD*) varied strongly among habitat species pools for most geological epochs, with the only exception being a low variation for the Late Cretaceous (100 – 66 Ma; Fig. 1(b)). Again, estimates of *stELDs* were not biased by polytomies and were very strongly correlated to averages across 100 trees that had been randomly dichotomized for all epochs, with the only exception being the last 5 Ma ($r^2 = 0.968$ – 0.999 for six oldest epochs, $r^2 = 0.548$ for the last 5 Ma; see Appendix S6 for *stELDs* values).

The overall phylogenetic age structures are much more complex than can be inferred from mean lineage ages. For instance, a habitat type can contain a species pool with significantly high diversities of lineages dating back to both ancient and recent epochs (Fig. 1(b), see Appendix S7 for details). Habitat types hence can act as museums, or as cradles of evolutionary history, or as both, i.e. they contain species pools with significantly increased diversities of lineages dating back to either of the Mesozoic epochs, to either of the Neogene epochs, or to both, respectively (see examples in Fig. 1(b) and Appendix S8).

The function of a habitat to contain high diversities of lineages dating back to a particular epoch can be explained by the abiotic environmental conditions in this habitat type. We used two approaches. First, we visually compared LTT plots for the ten most dry and ten most wet habitat types (Fig. 2(a), results for all habitat types are given in Appendix S4; moisture of

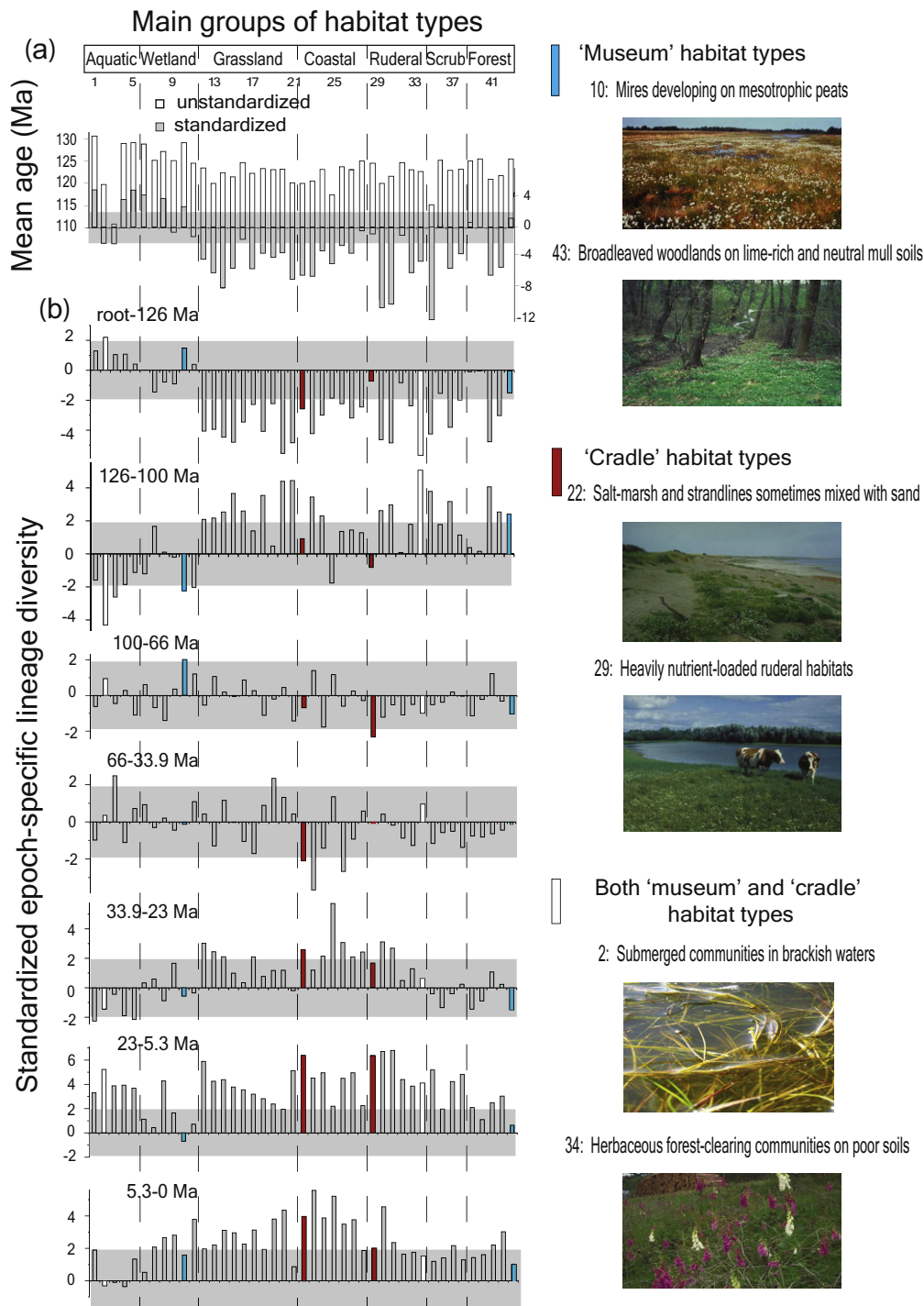


Figure 1 Present habitat types contain different levels of evolutionary heritage (43 habitat types grouped into seven main types; habitat types are named and defined in Appendix S2). (a) Habitat types differ in mean lineage ages (MLA). Ages are unstandardized for species richness (given in Ma, on left axis, and as open vertical bars) or are richness-standardized (given as effect sizes on the right axis, and as grey vertical bars), corresponding respectively to MLA and standardized MLA (stMLA) in the text (see Methods). The horizontal grey area indicates 95% confidence interval of a null model (further details in Appendix S5). (b) Habitat types differ in diversities of lineages dating back to different epochs. Diversities are standardized by species richness ('standardized epoch-specific lineage diversity', or stELD in the text; see Methods and further details in Appendix S6) and are represented as grey vertical bars. Epochs are defined in Ma and are indicated above each of the corresponding panels. Horizontal grey areas indicate 95% confidence intervals of epoch-specific null models. Note that diversities of lineages dating back to a given epoch are beyond null-expectations in most of the habitat types. Habitat types may act as 'museums' by containing high lineage diversities dating back to ancient epochs (defined as Mesozoic, i.e. > 66 Ma). Habitat types may act also as 'cradles' by containing high lineage diversities dating back to relatively recent epochs (Neogene and Quaternary, i.e. < 23 Ma). Multiple habitats act as both, some as neither; illustrated examples are indicated by open and coloured/shaded vertical bars (further details in Appendix S8).

habitat types was approximated through their ground water levels). Species pools from wet and from dry habitats show major differences in structure of their LTT plots, with very different (unstandardized) diversities of lineages dating back to very ancient or to very recent time slices (5 Ma each). High diversities of lineages dating back to the oldest geological epoch are contained specifically in the most wet habitats, whereas high diversities of lineages dating back to the second oldest geological epoch are contained in the most dry habitats (Figs. 2(a,b)).

In the second approach, we regressed, for each epoch, lineage diversities contained by the different habitat types (*stELDs*, as in Fig. 1(b)) against abiotic characteristics of these habitat types. In simple regression analysis we confirmed relationships to soil moisture found in the first approach and showed that these are highly linear and hence do not only reflect the extreme effect of a few particularly old mesangiosperm lineages in aquatic habitats (Fig. 2(c)). For lineage diversities dating back to 126 Ma and older we again found an increase with present habitat moisture, for lineage diversities dating back to 100 – 126 Ma we found a decrease (Fig. 2(c)). In multiple regression analyses we included four further environmental factors (light, soil phosphorus, soil pH, temperature). Again, we found that the same environmental factor may be associated with high diversities of lineages dating back to both ancient and recent but not intermediate epochs (Table 1; note that these results were also robust to randomly resolving polytomies as reported in Appendix S9). This explains existence of habitat types that are both ‘museum’ and ‘cradle’ in Fig. 1(b). Environmental factors were much less strongly related to lineage diversities when these were quantified per random or ‘naïve’, equal-sized age intervals and not based on distinct geological epochs characterized by distinct paleoenvironments (Appendix S10; references used in Supplementary Materials are cited in Appendix 1).

DISCUSSION

In this study we tested for differences in phylogenetic age structure of species pools of present habitat types from a regional flora, applying phylogenetically and ecologically highly resolved data. Our results confirm the ‘museum’/‘cradle’ hypothesis: just like species pools of biogeographic regions, much smaller species pools of different habitat types within a region significantly differ in their phylogenetic mean ages. However, our results also show that functions of habitats go beyond the dichotomy of ‘museums’ and ‘cradles’: lineages dating back to a given geological epoch are today contained in distinct habitat types. Mean ages of incumbent lineages do not reflect these differences in representation of distinct epochs, mean age is hence not representative of the age distribution. We stress that any extant Angiosperm has an ancestor in any of the epochs considered. High diversity of lineages dating back to a particular epoch is hence not simply the result of presence of one particularly basal or recent branch of the Angiosperm tree. Instead, there are in each habitat type multiple of these major branches, each characterised by an increased number of lineages from the particular epoch. Finding a pattern in lineage diversities that are specific to geological epochs is not surprising. Epochs were defined by geologists among others based on speciations and extinctions, i.e. on the two processes controlling diversification. Past epochs, hence, must leave some trace in the shape of the overall phylogeny of a lineage. However, our study does not focus on the overall phylogeny. It shows that different epochs from this phylogeny are very differently represented within different habitats. Existence of such differences and explanations cannot simply result from the way epochs were defined. Finally, our results also confirm the hypothesis that present-day abiotic environments control the diversity of lineages dating back to a given geological epoch. Variation in habitat-specific environmental parameters explained up to 75% of the variance in epoch-specific diversity of lineages from correspondent habitat types (Table 1)

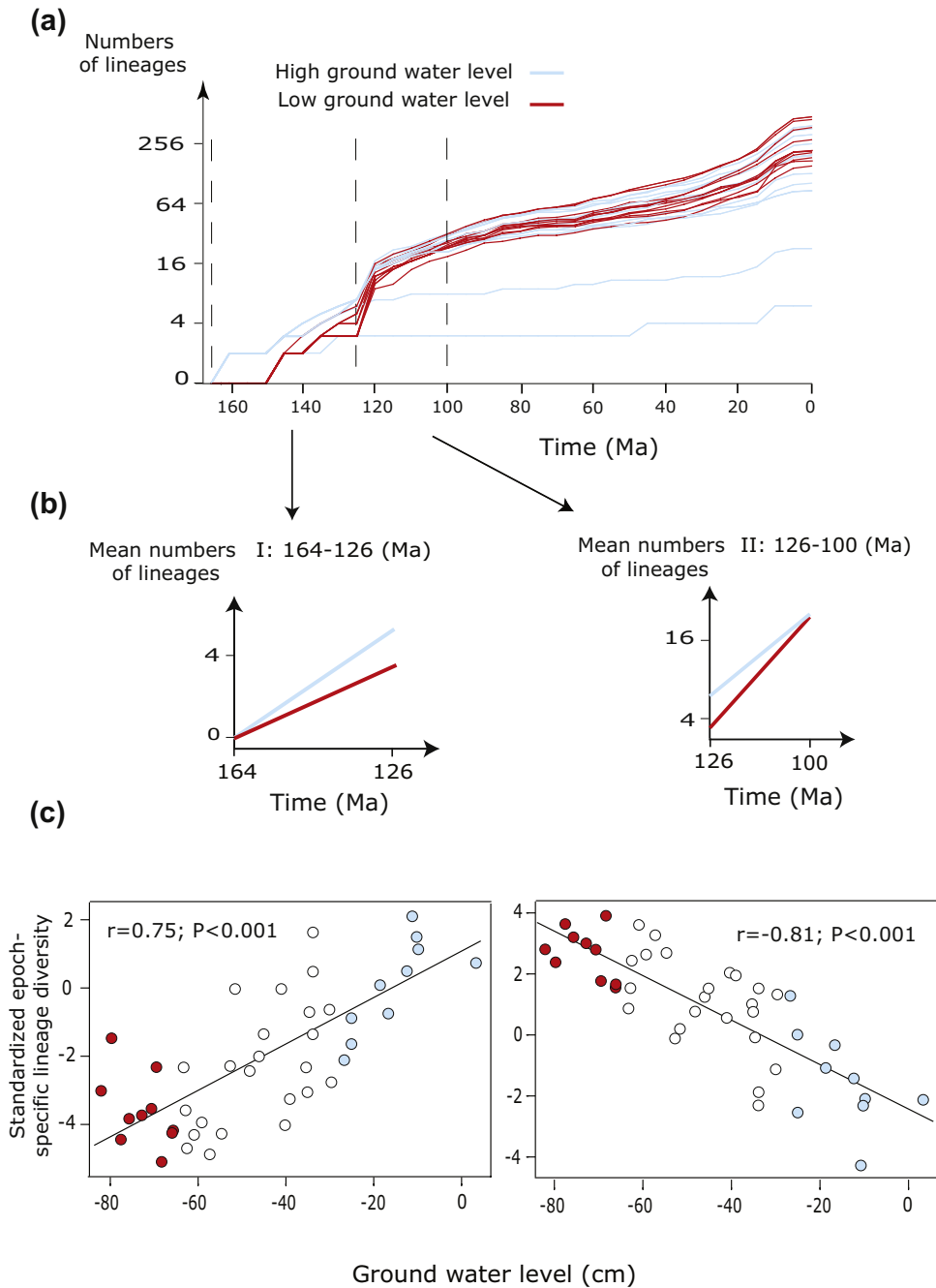


Figure 2 The soil moisture of habitat types is associated with a high diversity of lineages dating back to the oldest epochs. (a) Log_2 -transformed lineages-through-time plots for species pools from the 10 wettest habitat types (blue/light grey curves) and the 10 driest habitat types (red/dark grey curves), with moisture being inferred from ground water level. I and II indicate the most ancient and the second most ancient epochs in the evolution of angiosperms (I, between the root in the Jurassic to the Barremian/Aptian Ages boundary in the Early Cretaceous; II, until the Early/Late Cretaceous boundary). (b) Increments of log_2 richness of lineages dating back to the ends versus the beginnings of epochs I and II, richness being averaged separately across species pools of the wettest and driest habitat types. (c) Relationships between moisture of all 43 habitat types to diversities of lineages dating back to epochs I and II (i.e. the above lineage diversity increments standardized by present species richness, 'stELD' parameter). Habitat types belonging to the moist and dry groups presented in (a) are identified as blue/light grey and red/dark grey, respectively, intermediate habitat types (not presented in (a)) are in white. See Table 1 for multiple analyses accounting for multiple environmental variables in addition to moisture.

Table 1. Relationships between diversities of lineages of habitat types dating back to a given epoch (standardized, ‘*stELD*’ parameter), and the abiotic characteristics of these habitat types: light availability, temperature, ground water level, soil pH, and soil phosphorus availability (one of the main drivers of soil fertility). The relationships were analyzed for each of the seven epochs using linear multiple regressions with best subset search. Each line represents hence a single analysis. (See Fig. 2(c) for exemplary simple regression analyses.) Numbers are t-values for each independent variable included into the model; ‘—’ indicates a variable has been excluded from the model; R² indicates explained variance of the multiple regression model. Levels of significance: P<0.1 – #, P<0.05 – *, P<0.01 – **, P<0.001 – ***. Significant (P<0.05) associations are in bold.

Epoch (Ma)	Effect on diversities of lineages dating back to that epoch (t, P)					Total model R ² , P
	Light	Tempe- rature	Ground water level	Soil pH	Soil phosphorus	
164 – 126	—	-1.32	4.64***	-1.07	4.04***	0.75***
126 – 100	—	1.38	-5.93***	—	-1.36	0.68***
100 – 66	2.50*	—	—	-2.39*	—	0.22*
66 – 33.9	-4.59***	—	4.96***	—	-4.61***	0.41***
33.9 – 23	2.23*	—	-1.81#	2.50*	-1.65	0.59***
23 – 5.3	—	3.05**	-2.81**	2.11*	—	0.60***
5.3 – 0	7.18***	-1.99#	-4.98***	1.64	—	0.64***

Our results beg the question: Do phylogenetic age structures represented today in habitats of different abiotic environmental conditions reflect past diversifications in equivalent abiotic environments? Such a link may be unexpected given the recent drastic changes of habitats due to Quaternary climatic fluctuations and human impact. On the other hand, the key abiotic constraints on plant performance in present habitat types (i.e. light and nutrient availability, moisture, pH) are probably similar to those that have existed already in earlier epochs, independent of the natural or anthropogenic drivers of these constraints. In fact this similarity between past and present abiotic constraints is the ultimate cause of phylogenetic signal observed for Dutch angiosperms in their response to these abiotic constraints (Prinzing *et al.*, 2001)

We have two types of evidence that phylogenetic age structures in contemporary habitats may reflect past diversifications in similar abiotic environments. First, we found that relationships between present-day abiotic environment and the diversity of lineages dating back to particular periods became significantly less pronounced when these periods were defined as random or as ‘naïve’ (equal-sized) age intervals and not based on distinct geological epochs characterized by distinct environments (Appendix S10). Second, we explored whether warm or cool habitat types tended to contain lineages with high diversities dating back to globally warm or cool epochs, respectively, and whether dry or moist habitat types tended to contain high diversities of lineages dating back to globally dry or moist epochs, respectively. For this

purpose we used pertinent recent paleoclimatic reconstructions available for the more recent part of the time period considered, the Cenozoic (from 66 Ma to present, Zachos *et al.*, 2001; Dupont-Nivet *et al.*, 2007), and compared them with results of our regression analyses (Fig. 3). We found that our observation that warm habitat types contain high lineage diversities dating back to the Miocene indeed corresponds to warm paleoclimates during this epoch. Moreover, the high lineage diversities dating back to the last five million years contained in cold habitats correspond to a period of considerable global cooling and extensive continental glaciations. Also, high lineage diversities contained in dark and moist habitats and dating back to the Paleocene/Eocene correspond to a period of moist climate and boreotropical vegetation in the Northern Hemisphere (Reid & Chandler, 1933). In a sharp contrast, high diversities of lineages dating back to the several latest epochs (the last 34 million years), today contained in open and dry habitats, correspond to a period of major aridification of temperate regions (Jacobs *et al.*, 1999; Dupont-Nivet *et al.*, 2007).

We stress that the above considerations linking numbers of lineages from different epochs in different habitats to paleoenvironments, and mechanisms of diversification remain speculative. In particular, a relationship of present warm (or moist) environments to high diversity of lineages from warm (or moist) epochs may result from (i) increased speciation rates in warm (or moist) environments during these early epochs, (ii) increased extinction rates in later, cool (or dry) environments during the more recent epochs. The latter explanation has indeed been suggested based on paleobotanical data (Latham & Ricklefs, 1993; Willis & Niklas, 2004). Acknowledging this uncertainty, we note that it is common to many studies on net diversification rates (Quental & Marshall, 2010). A possible solution might be to obtain data on relative speciation and extinction rates based on complete and well-resolved phylogenies, rich fossil record, and well-characterized paleoecological environments from different places across the globe (Pennington *et al.*, 2004)

The data should focus not only on climatic, but also on soil characteristics of paleoenvironments, and account for different ranges and dispersal capacities of species within regions. We are not aware of such data for angiosperms. However, this uncertainty does not influence our conclusion that particular current habitat environments can maintain lineages dating back to epochs of particular paleoenvironments.

Identification of ‘museums’/‘cradles’ among habitat types within a region can help in prioritizing conservation efforts given the limited resources available and our failure to meet the international ‘biodiversity 2010’ target (Mace *et al.*, 2010). Habitats containing evolutionary heritage from oldest geological epochs might be considered particularly valuable and their decline would be particularly alarming. Such an approach would resemble that of phylogenetic endemism which accounts for geographic rarity of the lineages (Rosauer *et al.*, 2009; Mishler *et al.*, 2014), but requires a geographically much larger sample to be properly calibrated. Obviously, it has to be verified in each region which habitat types are to be classified as ‘museums’, ‘cradles’, or both. Habitats containing lineages that diversified in warmer epochs might today serve as a pool of species potentially still carrying adaptations to such warmer climates. Conservation of these habitats might represent an ‘ecological insurance’. Although in some extreme cases such as succulent plants in dry habitats this was always obvious, in most cases we had until now no means of testing this prediction. In other habitats component lineages might be especially sensitive to climate change and face the risk of ‘running out of climate space’ (cf. Ohlemuller, 2011). Although speculative, this approach is equivalent to what is established practice in the conservation of the genetic heritage of wild relatives of crop species, where under a warming climate wild relatives in warm habitats have particularly high conservation value (Kremer *et al.*, 2013).

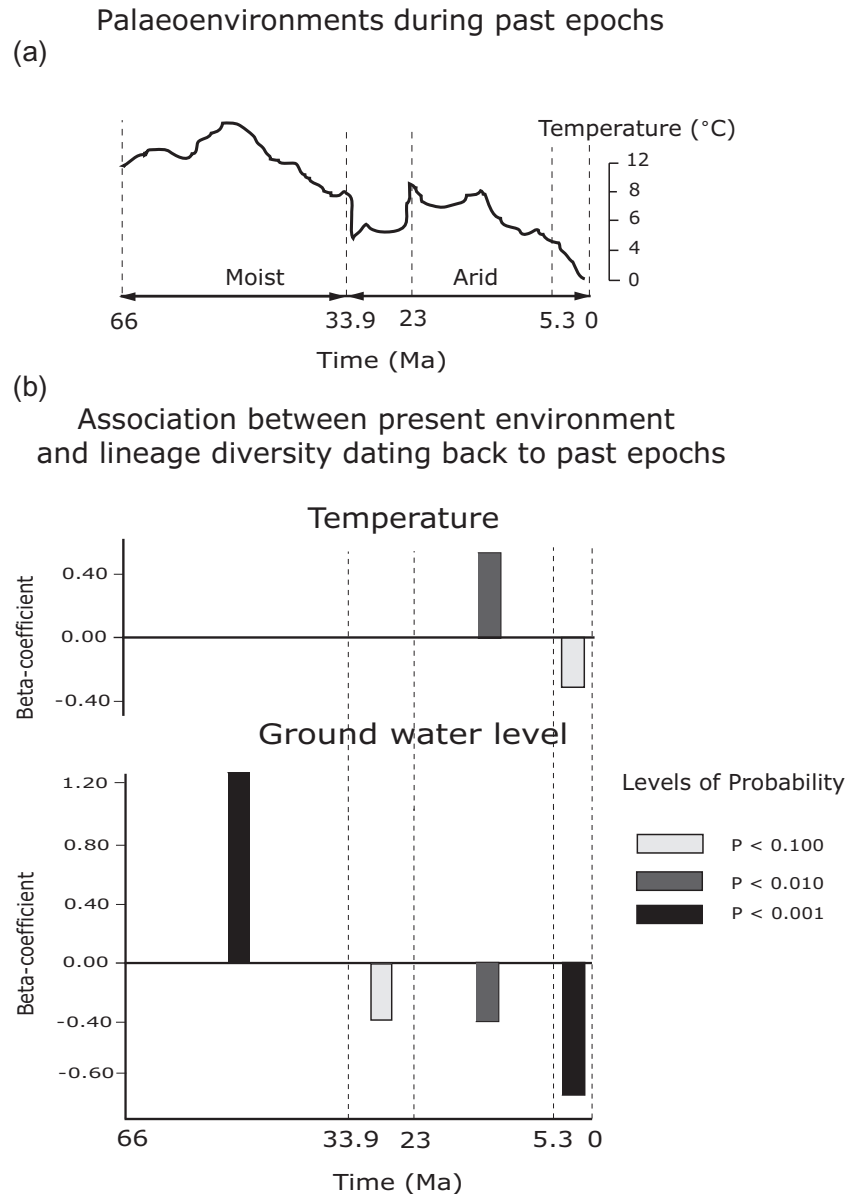


Figure 3 The paleoenvironment during a given epoch matches the environment that today contains high diversity of lineages from that epoch. (a) Global paleotemperatures (as deviation from present temperatures, Zachos *et al.*, 2001) and periods of moist and of arid paleoclimates in temperate regions (Reid & Chandler, 1933; Dupont-Nivet *et al.*, 2007) throughout the Cenozoic (66 Ma to present). Dashed lines depict epochs analyzed in Fig. 1 and Table 1. Note that climates from even older epochs are much less well known and hence not presented. (b) Relationships between present temperature or soil moisture of habitat types (upper and lower graph, respectively), and diversities of lineages dating back to each of the four epochs identified in (a). Relationships correspond to t- and P-values in the regression analyses reported in Table 1. Note that lineages dating back to warm or dry epochs tend to be preferentially contained in warm or dry habitat types.

CONCLUSIONS

Our findings indicate that within a given region habitats can function as ‘museums’ (particularly in wet habitats) or as ‘cradles’ (particularly in dry habitats), containing older or younger lineages, respectively. However, the classical ‘museum’/‘cradle’ dichotomy is often far too simple and linear to realistically describe the phylogenetic structure represented in different environments within a region, and a habitat can contain lineages from very different epochs. Specifically, the results suggest that within our study region habitat types with warm or dry environments seem to contain high lineage diversity from globally warm or dry epochs during the Cenozoic. Such a function of habitats was to our knowledge not appreciated so far. It is all the more impressive that such a function can be observed even within a region that is close to cool and moist limits of many plant lineages. The generality of this finding needs to be tested for other regions. Moreover, further research is needed to verify whether presence of lineages from the most recent epoch in some habitats corresponds to an increased ongoing production of new species.

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BIOSKETCH

I.V.B. is interested in impact of environmental changes on evolutionary processes in flowering plants. The team ‘Vegetation Ecology’ (W.A.O., G.W.W.W., S.M.H.) at Alterra Wageningen University and Research has a broad scope in disciplines relating to vegetation ecology and eco-informatics. AP and collaborators at Ecobio Unit at University Rennes 1 study ecology of diversification.

SUPPLEMENTARY ON-LINE MATERIAL

Appendix S1 Justification of studying lineage compositions of habitat types within a region

Appendix S2 Estimation of abiotic species indicator values and environmental characteristics of Dutch habitat types

Appendix S3 Reconstruction of a dated phylogeny of species of Dutch angiosperms

Appendix S4 Lineages-through-time plots of habitat species pools of Dutch angiosperms

Appendix S5 Estimates of standardized Mean Lineage Ages

Appendix S6 Estimates of standardized Epoch-specific Lineage Diversities

Appendix S7 Phylogenetic age structure of habitat species pools of Dutch angiosperms does not correspond to their mean lineage ages

Appendix S8 Classification of habitat types into ‘museum’, ‘cradle’, and both ‘museum’ and ‘cradle’ categories

Appendix S9 Multiple regression analyses of relationships between epoch-specific lineage diversities based on 100 trees with randomly resolved polytomies and the abiotic characteristics of habitat types

Appendix S10 Defining age intervals randomly or equally instead of based on geological epochs: consequences for relationships between environment and *stELD*

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