



Anthropogenic threats to evolutionary heritage of angiosperms in the Netherlands through an increase in high-competition environments

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Abstract: Present biodiversity comprises the evolutionary heritage of Earth's epochs. Lineages from particular epochs are often found in particular habitats, but whether current habitat decline threatens the heritage from particular epochs is unknown. We hypothesized that within a given region, humans threaten specifically habitats that harbor lineages from a particular geological epoch. We expect so because humans threaten environments that dominated and lineages that diversified during these epochs. We devised a new approach to quantify, per habitat type, diversification of lineages from different epochs. For Netherlands, one of the floristically and ecologically best-studied regions, we quantified the decline of habitat types and species in the past century. We defined habitat types based on vegetation classification and used existing ranking of decline of vegetation classes and species. Currently, most declining habitat types and the group of red-listed species are characterized by increased diversification of lineages dating back to Paleogene, specifically to Paleocene-Eocene and Oligocene. Among vulnerable habitat types with large representation of lineages from these epochs were sublittoral and eulittoral zones of temperate seas and 2 types of nutrient-poor, open habitats. These losses of evolutionary heritage would go unnoticed with classical measures of evolutionary diversity. Loss of heritage from Paleocene-Eocene became unrelated to decline once low competition, shade tolerance, and low proportion of non-Apiaceae were accounted for, suggesting that these variables explain the loss of heritage from Paleocene-Eocene. Losses of heritage from Oligocene were partly explained by decline of habitat types occupied by weak competitors and shade-tolerant species. Our results suggest a so-far unappreciated human threat to evolutionary heritage: habitat decline threatens descendants from particular epochs. If the trends persist into the future uncontrolled, there may be no habitats within the region for many descendants of evolutionary ancient epochs, such as Paleogene.

Keywords: abiotic and biotic constraints, biodiversity conservation, decline of habitat types, epoch-specific phylogenetic diversification, paleoecological inference, Paleogene

Amenazas Antropogénicas para la Herencia Evolutiva de las Angiospermas en los Países Bajos a partir del Incremento en los Ambientes de Competencia Elevada

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Article impact statement: A new method shows that a regional flora is losing heritage of oldest geological epochs by losing habitats of low competition intensity.

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Resumen: La biodiversidad actual abarca la herencia evolutiva de las épocas de la Tierra. Los linajes de épocas particulares se encuentran con frecuencia en hábitats particulares pero desconocemos si la declinación contemporánea de los hábitats amenaza a la herencia de una época en particular. Nuestra hipótesis supone que dentro de una región determinada, los humanos son una amenaza específica para los hábitats que albergan linajes de una época geológica particular. Suponemos esto pues los humanos amenazan a los ambientes y a los linajes que se diversificaron durante estas épocas. Diseñamos una nueva estrategia para cuantificar, por tipo de hábitat, la diversificación de los linajes de épocas distintas. Cuantificamos para los Países Bajos, una de las regiones mejor estudiada florística y ecológicamente, la declinación de los tipos de hábitat y de especies durante el siglo pasado. Definimos los tipos de hábitat con base en la clasificación de la vegetación y usamos las jerarquías existentes de la declinación de clases y especies de vegetación. Hoy en día, la mayoría de los tipos de hábitat en declinación y el grupo de especies en lista roja se caracterizan por la diversificación incrementada de los linajes que datan del Paleógeno, específicamente el Paleoceno-Eoceno y el Oligoceno. Entre los tipos de hábitat vulnerables con una gran representación de los linajes de estas épocas encontramos a la zona sublitoral e intermareal de los mares templados y dos tipos de hábitats abiertos con deficiencia de nutrientes. Estas pérdidas de linaje evolutivo pasarían desapercibidas con las medidas clásicas de la diversidad evolutiva. La pérdida de la herencia del Paleoceno-Eoceno dejó de estar relacionada con la declinación una vez que contabilizamos la baja competencia, la tolerancia a la sombra y la baja proporción de especies no pertenecientes a la familia Apiaceae, lo que sugiere que estas variables explican la pérdida de herencia del Paleoceno-Eoceno. La pérdida de herencia del Oligoceno estuvo explicada en parte por la declinación de los tipos de hábitat ocupados por competidores débiles y especies tolerantes a la sombra. Nuestros resultados sugieren una amenaza humana para la herencia evolutiva que todavía no ha sido apreciada: la declinación del hábitat amenaza a los descendientes de épocas particulares. Si en el futuro las tendencias siguen sin ser controladas, puede que no haya hábitats en la región para muchos de los descendientes evolutivos de épocas antiguas, como el Paleógeno.

Palabras Clave: conservación de la biodiversidad, declinación de los tipos de hábitat, diversificación filogenética específica de la época, inferencia paleoecológica, limitaciones bióticas y abióticas, Paleógeno

摘要: 现有的生物多样性包含了地球纪元以来的进化遗产。来自特定地质时期的谱系通常在特定的生境中被发现,但是目前的生境丧失是否会威胁来自特定时期的进化遗产仍不得而知。我们假设在特定区域内,人为威胁影响着特定地质时期的特定生境。提出这一假设是因为在特定的地质时期,人类往往威胁着其自身主导的环境和当时多样化的谱系。我们设计了一种新方法量化不同时期不同生境类型的谱系多样性。荷兰是植物区系和生态研究最好的地区之一,我们量化了其在过去百年间生境类型和物种的丧失情况。我们基于植被分类来确定生境类型,并利用已有的植被类型及物种丧失的信息进行了排序。目前,大多数丧失的生境类型和列入红色名录的物种都具有古第三纪以来谱系多样性增加的特征,特别是在古新世-始新世和渐新世。在这些时期,有大量代表性谱系的脆弱生境类型包括温带海洋的次大陆架和真沿岸地带,以及两种缺乏营养的开放生境。这些生境中的进化遗产丢失在传统的进化多样性分析中不会被注意到。而如果将低竞争力、耐阴性和低比例非伞形科植物等因素纳入考虑,则古新世-始新世的进化遗产减少与生境和物种丧失无关,说明这些变量可以解释古新世-始新世时期的进化遗产的减少。此外,竞争力弱的植物和耐阴物种所占据的生境类型的丧失可以部分解释渐新世的进化遗产减少。我们的研究结果展示了人类对进化遗产的威胁:生境丧失威胁着特定时期的谱系后代,而这个问题目前尚未得到重视。如果这种趋势不受控制地继续发展,那么在这个区域内可能就不再有进化远古时代(如古第三纪)的许多谱系的生境。**翻译: 胡怡思; 审核: 聂永刚**

关键词: 非生物与生物制约, 生物多样性保护, 地质时期特异的系统发育多样化, 生境类型减少, 古生态推断, 古第三纪

Introduction

An important reason biological diversity is valued is that it represents the heritage left to humanity from life across time. Some lineages stem from old epochs and testify to the origins of present diversity in the environments of these epochs. Other lineages stem from recent epochs and indicate the trajectories of ongoing diversification in recent environments. Maintaining both might function as insurance against a rapidly changing world. Lineages of ancient and of recent origin sometimes occur in distinct regions, for example, angiosperms in New Caledonia versus the Cape Region, both of which are con-

sidered of conservation value (Jaffre et al. 1997; Forest et al. 2007). Within regions, lineages of ancient and recent origin can occur in different habitat types (e.g., angiosperms in Western European mires and salt marshes [Bartish et al. 2016]), albeit no conservation conclusions have been drawn so far.

Within any region, humans affect some habitat types more than others (Weeda et al. 2005; Rodríguez et al. 2007; Keith et al. 2015). We define *habitat type*, following Evans (2006), as a type of environment within a region distinguished by abiotic and biotic features that is recognizable by its vegetation. Consequences of habitat decline for species decline have been studied

extensively (e.g., Janssen et al. 2016). Decline of habitats likely also affects particular lineages (Purvis 2008) because lineages tend to conserve adaptations that permitted establishment, radiation, and survival in particular habitat types (i.e., phylogenetic conservatism of traits [Wiens & Graham 2005; Wiens 2011] and habitats [Prinzling et al. 2001]). However, it is unknown whether habitat decline affects the decline of lineages from particular epochs. Some qualitative observations suggest that the anthropogenically more affected habitats sometimes harbor particularly old lineages, such as the greatly declining natural habitats harboring the Mesozoic monotypic lineages *Ginkgo* and *Sequoiadendron* (Tang et al. 2012; Schmid & Farjon 2013). In contrast, declining seminatural grasslands in temperate regions harbor a wide range of particularly recent lineages (Dengler et al. 2014; Peronne et al. 2014; Bartish et al. 2016). We argue that there is a general relationship: human impact threatens habitat types that harbor lineages that stem from particular epochs.

Decline of those habitats that harbor evolutionary heritage from a particular epoch might result from either of 2 mechanisms. First, declining habitats might harbor declining lineages that originated during this particular epoch. For instance, humans threaten numerous lineages of Asteraceae and Orchidaceae according to red lists in Europe (i.e., Bilz et al. 2011). These lineages had their maximum diversification rates during particular epochs, diversified little across other epochs (Inda et al. 2012; Nie et al. 2016), and are more abundant in some habitat types than in others (Judd et al. 2007). Decline of these habitat types would lead to a decline of evolutionary heritage from these particular epochs. Second, declining habitats represent particular abiotic or biotic environments. If these declining environments dominated during a particular epoch, then lineages that originated during that epoch can be threatened due to disappearance of their origin environments. For example, anthropogenic deforestation is a major cause of extinctions of tree and herb lineages that diversified in understory environments. These were the most likely dominant environments of the Paleocene and the Eocene (Burnham & Johnson 2004; Kvaček 2010). Other environmental conditions humans threaten include high soil moisture or low soil fertility (Good & Beatty 2011; Verhoeven 2014)—conditions that were more pronounced in some epochs than in others (Behrensmeyer et al. 1992; Prinzling et al. 2001; Bartish et al. 2016).

Most investigations into human threats to evolutionary history focus on species or taxa rather than habitats as declining units, and all focus on diversity (e.g., distance among lineages) rather than diversification (e.g., numbers of lineages originating and surviving during a given geological epoch with its specific paleoenvironment). Some approaches focus on species and are used to determine whether species decline threatens entire

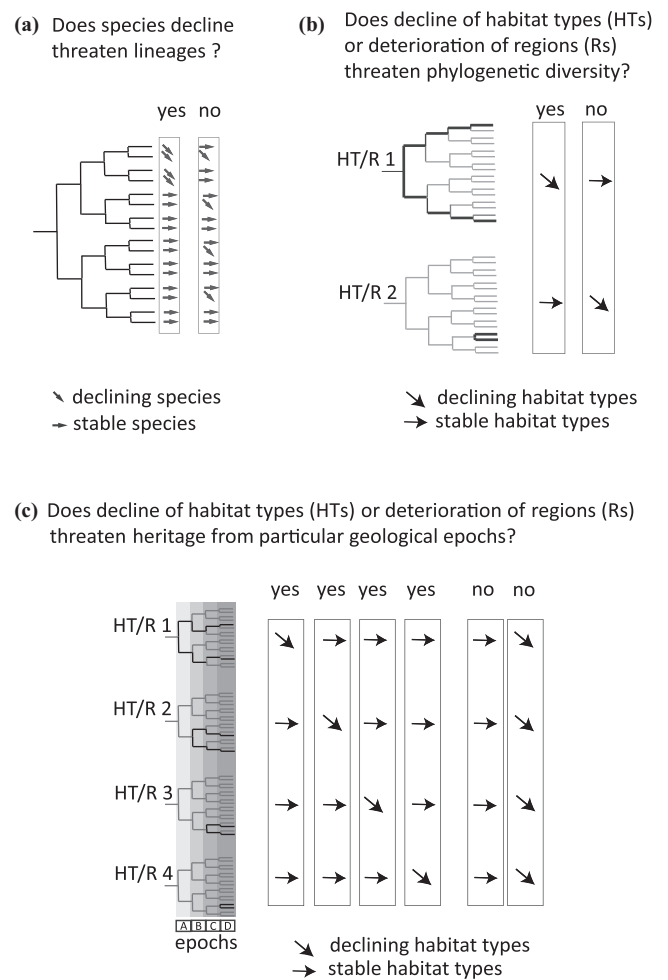


Figure 1. (a, b) Two classical approaches and (c) our approach to quantifying how human impact threatens evolutionary history. In (a), the focus is on decline of species, and in (b) and (c), the focus is on decline of habitats or deterioration of regions. Approaches (a) and (b) focus on lineages and their distances (i.e., diversity). Patterns are sometimes interpreted in terms of environmental history, but without direct evidence. In contrast, approach (c) focuses directly on diversification and known environmental history through the different geological epochs of Earth.

lineages (i.e., Do human-endangered species cluster in certain lineages) (e.g., Nee & May 1997; Lambert & Steel 2013; Faith 2015) (Fig. 1a). Other approaches focus on local communities in habitat patches and are used to determine whether communities in threatened habitat patches show particularly large phylogenetic diversity (Faith 1992; Pavoine et al. 2004; Winter et al. 2013) (Fig. 1b). However, neither of these approaches focuses on consequences of decline in habitat types for maintaining heritage from particular geological epochs and the corresponding paleoenvironments. All these

approaches focus on evolutionary distances (i.e., phylogenetic diversities) and most treat large evolutionary distances as evidence of high conservation value. This overlooks the value of maintaining the entire geological history of diversification of plants across multiple epochs of the geological history of the Earth (Fig. 1c). Such diversification per geological epoch could be used to characterize clades and compare threatened and nonthreatened clades or to characterize habitat types and compare threatened and nonthreatened habitats.

New methods allow one to partition evolutionary history across time. Focusing on diversity (i.e., phylogenetic distance), Pavoine et al. (2009) dissected phylogenies among intervals defined by the topology of the tree itself. Focusing on diversification (i.e., numbers of originating and surviving lineages), Bartish et al. (2016) dissected phylogenies according to geological epochs by identifying the standardized diversification of lineages dating back to each of these epochs (standardized epoch-specific lineage diversities [stELDs]). These authors identified phylogenies of the species pool for each habitat type within a region and then dissected these phylogenies according to epochs. They found that some habitat types function as museums of lineages that diversified during old epochs, others as cradles of lineages that diversified during recent epochs, or as both (see also Bartish et al. 2010). However, whether and why such epoch-specific lineage diversifications relate to habitat decline have not been investigated.

We hypothesized that within a given region, anthropogenic decline of habitats is a threat to evolutionary heritage from specific geological epochs (Fig. 1c). We also hypothesized that this may be so due to the selective impact of humans on either particular lineages or particular abiotic or biotic environments. We studied the flora of The Netherlands, a region that has seen dramatic impacts due to humans that almost entirely explain declines of habitat types during the recent century (Weeda et al. 2000, 2005). The Netherlands is also very well studied floristically and ecologically (Schaminée et al. 2012) and has a highly resolved, dated plant phylogeny (Hermant et al. 2012; Bartish et al. 2016). We calculated decline of habitat types and related it to measures of epoch-specific evolutionary heritage and to classical measures of evolutionary heritage. We then verified whether these relationships were explained by the presence of particular lineages or particular abiotic (soil, microclimate) or biotic (competitors, shade) environmental conditions. We also explored consistency between epoch-specific patterns of habitat decline and epoch-specific patterns of species threat. Given that habitat decline is the most prominent threat to plant species in The Netherlands (WWF Netherlands, 2015), threatened species and declining habitats should both represent lineages from the same epochs.

Methods

Habitat Types and Their Trends

We identified Dutch habitat types as vegetation classes and their species pools as in Bartish et al. (2016) (detailed in Supporting Information). We quantified trends (variation in area sizes) of habitat types during the 20th century based on data on vegetation associations from Weeda et al. (2000–2005): strong decline, >50% decline in occupied grid cell number (−2); decline, 25–50% (−1); stable, <25% change (0); increase, >25% increase (1). Because most vegetation classes consist of multiple associations, we averaged trends of associations within the corresponding vegetation classes (habitat types) to calculate our trend index (results in Supporting Information), which provides estimates of change in area sizes of Dutch habitat types during the 20th century. Negative values indicate decline and positive values indicate expansion of habitat types.

Diversification during an Epoch Represented in a Habitat Type

We reconstructed the phylogeny of angiosperms and defined geological epochs as explained in Bartish et al. (2016) (details in Supporting Information). We quantified diversification per epoch as reflected by standardized stELDs for each epoch and each habitat type, as in Bartish et al. (2016), as the increase in \log_2 -transformed numbers of lineages between the beginning and the end of the geological epoch (see Supporting Information). The index thus summarizes diversification (i.e., origin and survival across lineages of a particular species pool at a particular epoch). Using \log_2 -transformed numbers permits a focus on proportional rather than absolute increases of lineage numbers. Bartish et al. (2016) standardized their estimates of ELDs with null expectations for habitat species pools of a given number of species from a regional species pool. Null expectations (phylogeny shuffle option in PHYLOCOM 4.1 [Webb et al. 2008]) of ELDs were computed for all species pools and all epochs as means across 999 random samples of a given number of species from the total tree of Dutch angiosperms. Bartish et al. (2016) used a modified version of LTTR module of Phylocom 4.1 (<https://github.com/markbartish/st-eld>). For each epoch in each habitat species pool, they calculated differences between observed and means of null-expected ELDs, divided this by standard deviation of the null-expected ELDs to yield richness-independent stELD values. Without such standardization, epochs that produced many lineages would be ranked high for all habitat types and habitat types with many species would be ranked high for all epochs (species richness varied by 2 orders of magnitude among habitat species pools). Moreover, such standardization allows integration of particular, but partly

unknown, properties of the index into the null model. What is important for our analyses is the variation of stELDs among habitat types for a given epoch, rather than the absolute value of a given stELD. To account for phylogenetic uncertainty, Bartish et al. (2016) produced 100 trees in which remaining polytomies in the basic dated tree were randomly resolved in MESQUITE 3.03 (Maddison & Maddison 2015) with the option randomly resolve polytomies in this software. Bartish et al. (2016) then calculated stELDs for each of these trees and each geologic epoch in the modified version of PHYLOCOM 4.1. Values of stELDs calculated from a dated phylogenetic tree with partly unresolved (PU) and partly randomly resolved polytomies are in Supporting Information.

Diversification during an Epoch Represented among Threatened Species

We calculated stELDs for threatened species (i.e., species red listed as regionally extinct, critically endangered, endangered, or vulnerable according to Floron 2000) at roughly the end of the period across which habitat trends have been described. For each epoch, we verified the position of the unsigned stELD in the probability distribution of Z values (e.g., the probability of finding a value larger than 1.96 [unsigned] is 5%) (Statistica version 8, Statsoft Maisons-Alfort, France). We considered the relationship between stELDs and trends of habitat types in the 6 epochs we retained for the analysis across habitat types (see “Statistical Analyses” and Supporting Information). We verified whether epochs for which the across-habitat relationship between stELD and decline were significant also showed a significant stELD of red-listed species.

Commonly Used Measures of Evolutionary Heritage

We quantified, for each species pool, log₂-transformed species richness; branch lengths in a phylogenetic tree connecting the species in a habitat species pool (phylogenetic diversity [PD]); negative mean phylogenetic distances across all pairs of species (net relatedness index [NRI]); and negative mean nearest phylogenetic distances across pairs of most closely related species (nearest taxon index [NTI]) (Faith 1992; Webb et al. 2008). The PD, NRI, and NTI were standardized by species number in Phylocom 4.1 with the same null model as for stELDs (i.e., phylogeny shuffle option). Results for each habitat type are in Supporting Information.

Inferring Environments in Different Habitat Types

We characterized abiotic conditions (ground water level, soil reaction, soil phosphorus, and temperature) and biotic conditions (shading and competition pressure) as

the means across local communities and in local communities by means across indicator values of species (Bartish et al. 2016 & Supporting Information). Such an approach permits characterizing habitat patches that are too numerous for local comprehensive measurements and too small to be represented by climate or soil maps.

Statistical Analyses

We used multiple regression analysis (Statistica) to relate trends of habitat types (dependent variables) to the evolutionary heritage of their species pools (independent variables) (i.e., stELDs). We performed this regression analysis for each of the 2 types of stELDs (i.e., calculations based on unresolved or resolved phylogeny). We selected variables to reduce multicollinearity with Akaike information criterion (AIC) and performed outlier analysis as explained in Supporting Information.

We then included commonly used measures of evolutionary heritage into the analyses relating stELDs to trends of habitat types. This permitted exploration of whether stELDs of a given epoch are more strongly associated with trend than are commonly used measures of evolutionary heritage. We then included environmental conditions in the initial analyses relating stELDs to trends with either abiotic or biotic variables as defined above. We finally included proportion of families in the initial analysis. The last 2 analyses permitted us to identify whether effects of stELDs were mediated via environment or via proportion of families, and hence, disappeared once these variables were included in the analysis. We could not include proportions of all 99 families of angiosperms in the region. Hence, we first searched for the families with significant ($p < 0.05$) association with trends (Supporting Information). We used proportions of Apiaceae, the only family identified under this selection criterion, in the multiple regression analyses explaining trend.

The numerous types of analyses were hierarchical, rather than multiple independent tests. Later analyses were used to explain the results in former analyses. If in an earlier analysis stELD from a particular epoch related to habitat trend and in a later analysis, this relationship disappeared after inclusion of an environmental preference or a family proportion, then this environment or family might explain the effect of the stELD from that epoch. We used plots of partial residuals to illustrate the strongest relationships of trends with particular independent variables.

Results

Habitat Decline and High Diversification from Paleocene-Eocene and Oligocene

Habitat types whose species pools represented high diversification of lineages in the Paleocene-Eocene

Table 1. Results of the multiple regression of trends in Dutch habitat types versus their epoch-specific lineage diversities (stELDs) accounting for and not accounting for commonly used measures of evolutionary heritage (i.e., species richness, phylogenetic diversity, net relatedness index, nearest taxon index); some abiotic environmental conditions (i.e., ground water level, soil phosphorus, soil reaction, temperature); shading and competition; and representation of families.*.

Variables in best models from different analyses	Estimate	Statistics of variables	
		LR χ^2	p
Epoch-specific lineage diversifications (stELDs)			
LR $\chi^2 = 13.93$; residual df = 33; $p < 0.008$			
stELD, the Jurassic-Early Cretaceous (164–126 Ma)	−0.070	3.168	0.075
stELD, the Late Cretaceous (99.6–65.5 Ma)	−0.100	1.607	0.205
stELD, the Paleocene-Eocene (66–33.9 Ma)	−0.134	5.880	0.015
stELD, the Oligocene (33.9–23 Ma)	−0.206	8.261	0.004
Commonly used measures of evolutionary heritage in addition to stELDs			
LR $\chi^2 = 17.68$; residual df = 29; $p = 0.001$			
stELD, the Paleocene-Eocene (66–33.9 Ma)	−0.148	3.840	0.050
stELD, the Oligocene (33.9–23 Ma)	−0.256	8.994	0.003
Species richness	0.993	4.414	0.036
Nearest taxon index	−0.165	1.521	0.218
Abiotic environmental conditions in addition to stELDs			
LR $\chi^2 = 16.09$; residual df = 29; $p < 0.007$			
stELD, the Late Cretaceous (99.6–65.5 Ma)	−0.071	0.691	0.406
stELD, the Paleocene-Eocene (66–33.9 Ma)	−0.150	6.627	0.010
stELD, the Oligocene (33.9–23 Ma)	−0.165	5.232	0.022
stELD, the Miocene (23–5.3 Ma)	0.143	4.558	0.033
soil reaction	−0.122	1.980	0.159
Shading and competition in addition to stELDs			
LR $\chi^2 = 26.05$; residual df = 27; $p < 0.001$			
stELD, the Paleocene-Eocene (66–33.9 Ma)	−0.083	2.939	0.087
stELD, the Oligocene (33.9–23 Ma)	−0.112	2.607	0.106
stELD, the Miocene (23–5.3 Ma)	0.043	0.485	0.486
competition	0.156	14.287	<0.001
shading	−0.444	6.484	0.011
Representation of families in addition to stELDs			
LR $\chi^2 = 18.32$; residual df = 31; $p = 0.001$			
stELD, the Jurassic-Early Cretaceous (164–126 Ma)	−0.086	4.971	0.026
stELD, the Paleocene-Eocene (66–33.9 Ma)	−0.085	2.329	0.127
stELD, the Oligocene (33.9–23 Ma)	−0.195	8.204	0.004
Apiaceae	10.181	4.476	0.034

*All analyses are based on 100 randomly resolved trees as explained in Methods (see Supporting Information for analyses based on partly unresolved phylogenies). Variables always selected by best subset with lowest Akaike information criterion value. See Fig. 2 for illustrations of the core results.

(66–33.9 Ma) and the Oligocene (33.9–23 Ma) had negative trends for both partly randomly resolved (PR) and for PU trees (Table 1, Figs. 2a & b, Supporting Information). Phylogenies of the 2 habitat types of extreme trends are in Figs. 3(a) and (b). The phylogeny of the greatly decreasing habitat type revealed much more diversification in the Paleocene-Eocene and the Oligocene than the greatly increasing habitat type. Even after including commonly used measures of evolutionary heritage (species richness and 3 indexes of phylogenetic diversity), diversification of lineages in the Oligocene was still related to habitat decline in analyses of both types of trees, whereas the signal of diversification of lineages in the Paleocene-Eocene and the relationship with species richness was mixed (Table 1, Fig. 2c, & Supporting Information). Low species richness was significantly related to habitat de-

cline in analyses of PR trees (Table 1 & Fig. 2c). The other commonly used measures of evolutionary heritage were not significant and mostly not included in the final model (PD was particularly strongly related to species richness: $p < 0.001$; $r^2 = 0.80$).

Species Threat and High Diversification from Paleocene-Eocene

Species listed as threatened on the Dutch red list represented strong lineage diversification in the Paleocene-Eocene epoch (stELD = 2.183, $p = 0.029$, phylogeny as in Fig. 3c), which is consistent with our results across habitat types. Red-listed species represented low lineage diversification in the Jurassic-Early Cretaceous and Miocene (stELDs = −2.280 and −2.772, $p = 0.023$ and 0.006, respectively). The relationships with high

diversification were detected across habitat types for only the Miocene, only the partly resolved phylogeny, and only after including environmental conditions (Table 1 & Fig. 2d). The former analyses were based on a single set of species, those that are red-listed, and hence could not account for multiple epochs synchronously, contrary to the above across-habitat-type analyses.

Accounting for Environmental Conditions

In the presence of 4 abiotic environmental variables included into the analyses, stELDs from the Paleocene-Eocene and the Oligocene were again included in the best models and associated with decline (for both types of trees [Table 1 & Supporting Information]). Moreover, a new significant relationship appeared in results with the PR tree: high lineage diversifications in the Miocene were positively associated with trend (Table 1 & Fig 2d).

Biotic environmental variables had more of an effect on association of evolutionary heritage with trend than abiotic. In declining habitats species competitiveness ranked low and shade tolerance ranked high (Table 1, Figs. 2e and f, & Supporting Information). Lineage diversifications in the Paleocene-Eocene were now at most marginally significantly related to decline (in analyses of PR trees, $p = 0.087$ compared with $p = 0.015$ in the initial analysis) (Table 1). Lineage diversifications in the Oligocene were at most moderately significantly related to habitat decline (in analyses of PU trees, $p = 0.033$ compared with $p = 0.003$ in the initial analysis [Supporting Information]). Declines of habitats with little competition pressure or high shading hence seemed to partly explain the relationship between decline of habitats and diversification of lineages in the Paleocene-Eocene and possibly Oligocene described above.

Accounting for Lineage Identity

Apiaceae were the only family whose proportion was associated with trend in results of the univariate analyses (Supporting Information). When proportion of Apiaceae was included together with stELDs, strong habitat decline remained significantly associated with high diversification of lineages in the Oligocene, but not with diversification of lineages in Paleocene-Eocene (Table 1, Fig. 2g, & Supporting Information). Hence, low proportion of Apiaceae in declining habitats might have partly explained the relationship between habitat decline and high lineage diversification in the Paleocene-Eocene. We found a new relationship: habitats with high diversification in the oldest epoch, the Jurassic-Early Cretaceous, were declining in analyses of PR trees (Table 1 & Fig. 2h).

Discussion

Epoch-Specific Lineage Diversities as a Useful Tool to Identify Consequences of Habitat Decline

Habitats that declined in the Netherlands in the last century maintained lineages that diversified in the Paleocene-Eocene and Oligocene (i.e., the Paleogene epochs, 66–23 Ma). Consistently, we found a signal of high diversification in Paleocene-Eocene also with a completely different approach in which we analyzed overly simply epoch-by-epoch the phylogeny of threatened species. Neither of the most commonly used indexes of phylogenetic diversity was informative, and species richness was uninformative in analyses based on the PU tree. Epoch-specific diversifications in habitat types thus emerged as a useful addition to the commonly used set of phylogenetic tools in conservation. These stELDs can help identify museums, cradles, and combinations of museums and cradles of lineages among regional habitat types (Bartish et al. 2016). We found that specific ancient geological epochs from the Paleogene are important identifiers of loss of evolutionary heritage caused by anthropogenic habitat decline. It remains to be seen whether future improvement of knowledge of phylogenetic relationships and higher precision in dating estimates will change our conclusions. Our preliminary comparison of results based on phylogenetic trees with different degrees of resolution suggests that the remaining phylogenetic uncertainty may be an important, but not a critically limiting factor in similar analyses.

Declining Habitat Types and Maintenance of Lineages from Paleocene-Eocene and Oligocene

The high diversification of lineages in the Paleocene-Eocene and Oligocene in declining habitats can be statistically partly explained by high shade tolerance and in particular low competitiveness of species in declining habitats. During the Paleocene-Eocene, angiosperm forests expanded across the globe (Pennington et al. 2004; Bartish et al. 2011; Thomas et al. 2015). Herbaceous species have to tolerate the shade in such forests because they cannot outcompete the trees for light. Thus, the dominant forest environments of this epoch could have been the origin of herb lineages that tolerate shade and competition by trees. In contrast, during the Oligocene, average environments were less shady (Bartish et al. 2016). Temperatures had stabilized at a relatively cool level (Zachos et al 2001), and disturbances by grazing mega herbivores and by cold winters may have prevented competitive replacement of herbs. These environments could have again triggered the origin of herb lineages with low competition capacities. If lineages of Paleocene-Eocene or Oligocene origin maintained their environmental preferences until today (Prinzing et al. 2001; Wiens 2011), one would expect that current

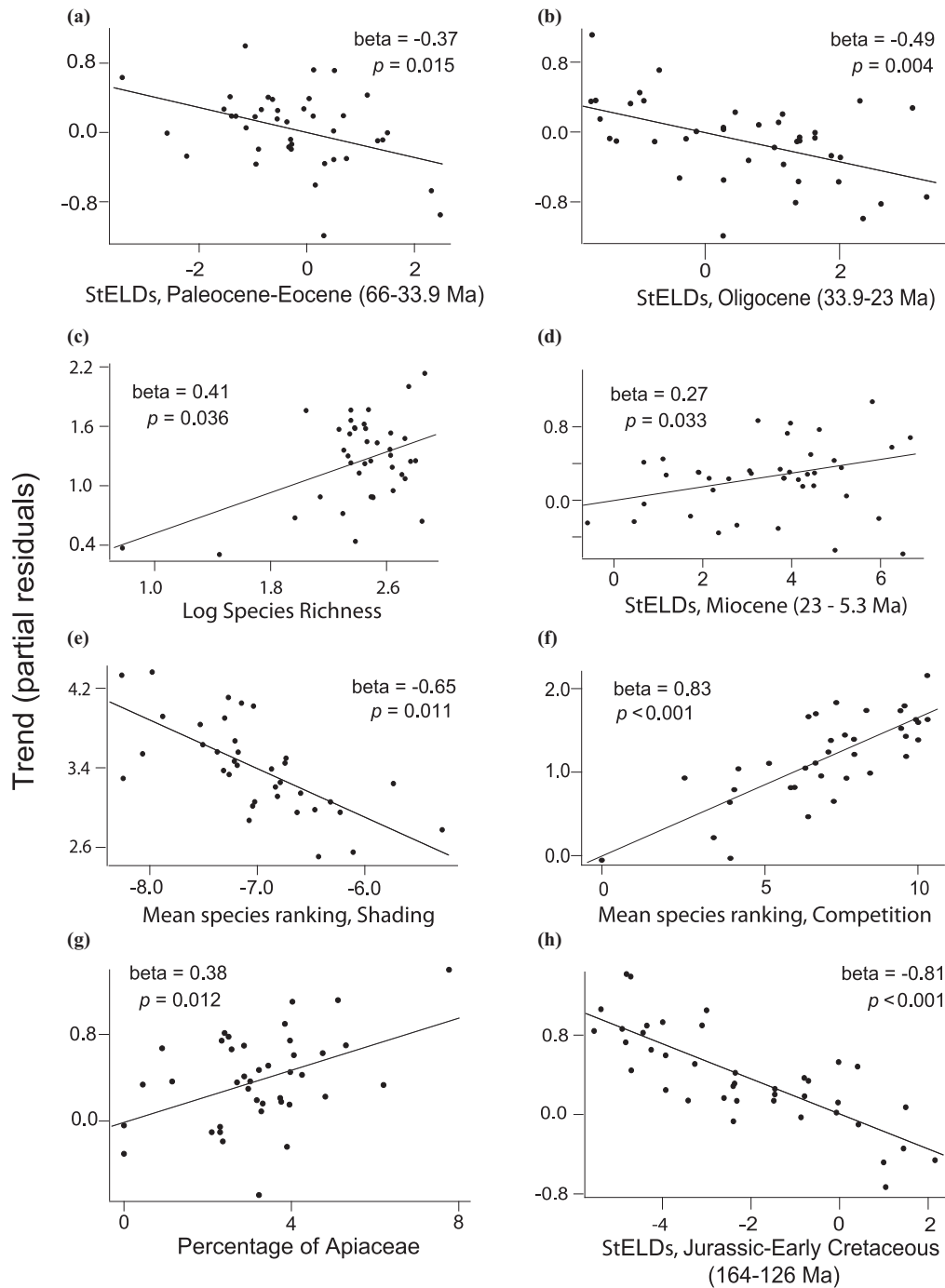


Figure 2. Relationships between trends in surface area of Dutch habitat types during the 20th century as a dependent variable and other properties of these habitat types: lineage diversifications in the (a) Paleocene-Eocene, (b) Oligocene, (d) Miocene, and (h) Jurassic-Cretaceous of the species pools; (c) species richness of the species pools; (e) shading and (f) competition inferred from species requirements and traits; and (g) representation of Apiaceae in the species pools. Trends are given as partial residuals accounting for other covariables in the respective multiple regression analysis (see Table 1 for details). Results of the analyses reported here are based on 100 randomly resolved trees. Negative trends indicate decline.

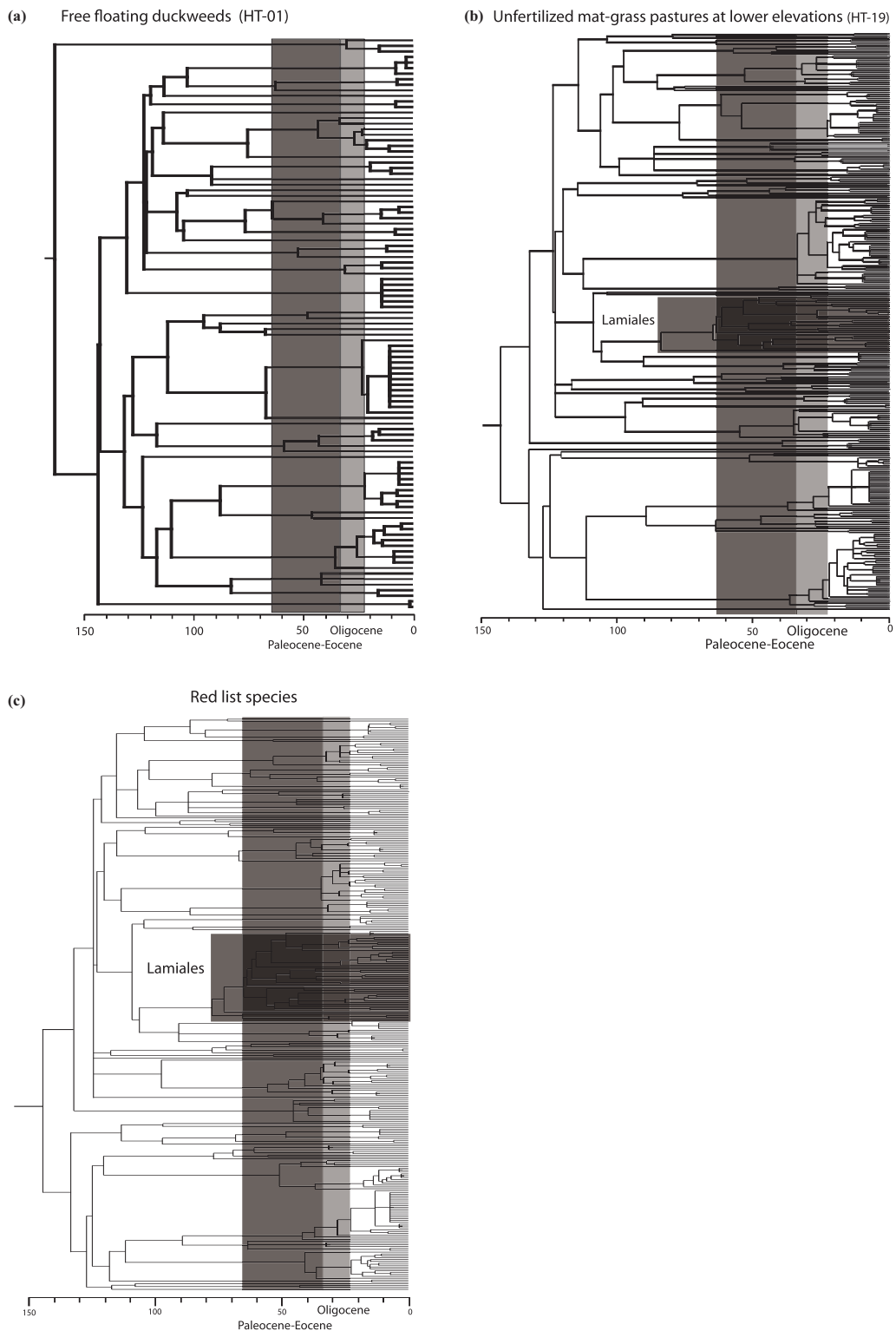


Figure 3. Dated phylogenies of (a) the species pool of the habitat type of most positive trend of surface area during the 20th century (free floating duckweeds [HT-01, 103 species]), (b) the species pool of the habitat type of the most negative trend (unfertilized mat-grass pastures at low elevations [HT-19; 286 species] [HT-03 declined even slightly more than HT-19 and had a similar phylogenetic structure; however, HT-03 harbors only 6 species, rendering the phylogeny visually incomparable with that of HT-01]), and (c) threatened species (ranked as threatened on Dutch red-lists) (dark gray, the Paleocene-Eocene; light gray, the Oligocene). See Supporting Information for descriptions of habitat types.

habitats characterized by low competition capacities of herbs (or by shade) may have a high diversification of lineages from the Paleocene-Eocene and Oligocene. During the last century, the area occupied by habitats where competition among herbs is low has declined in The Netherlands. Heathlands and bare ground have disappeared due to gaseous nutrient emission and transformed to other land-cover types (Weeda et al. 2000–2005). Within forests, level of competition on the ground probably increased due to the effects of increased soil fertility and the maturation of relatively young forests (Weeda et al. 2000–2005).

Expanding Habitat Types and Maintenance of Lineages That Diversified in the Miocene

Expanding or stable habitats maintained lineages that diversified in 1 of the 2 most recent epochs, the Miocene (Fig. 2d), when abiotic conditions were included as covariables (Table 1). The analysis of the phylogeny of red-listed species gave the same result. Together with the species richness of expanding habitat types, these results suggest that outcomes of recent speciation and radiation of lineages are overrepresented in expanding habitat types. These results are consistent with those of Prinzing et al. (2004), who found that large range size and high occupancy mainly occur among young species. The relationship between habitat expansion and high lineage diversification in the Miocene was not mediated by any of the other variables we accounted for, and we can only speculate about other relevant variables. For instance, grasslands with mammalian herbivores dominated the Late Miocene and are roughly similar to many present-day expanding Dutch habitats (Behrensmeyer et al. 1992). Also, the sheer recentness of this epoch means that extant, closely related species often originated in the Miocene. Such closely related species may mutually help each other, which would increase resilience to anthropogenic stress and disturbance (Prinzing et al. 2016; Prinzing et al. 2017). All these processes and interactions may contribute to the maintenance of vegetation of the Miocene origin and of the habitats this vegetation forms.

Representation of Apiaceae in Expanding Habitat Types

The high diversification of lineages in the Paleocene-Eocene in declining habitats can also be explained statistically by weak representation of Apiaceae in declining habitat types. Apiaceae may benefit from anthropogenic soil fertilization, efficiently defend themselves against anthropogenic grazing, and avoid anthropogenic mowing (Grime et al. 1988). Apiaceae can dominate vegetation cover and thereby engineer their habitat, so their success could be a cause not just a consequence of the expansion in habitats rich in these families.

Implications for Conservation

We argue that to preserve the evolutionary heritage from past epochs, it might not be sufficient to protect particular hotspot regions, which may function as museums or cradles. Protection of entire large and densely populated regions is not practical. It may be necessary, and more practical, to protect within each region (hotspot or coldspot) specific habitat types that maintain lineages that diversified throughout particular ancient epochs with specific environments. In particular, high diversification of lineages in the Paleogene was associated with decline in our study. Given the limited resources available and the failure to meet the Biodiversity 2010 target (Mace et al. 2010), identification of these habitat types can help in the prioritization of conservation across habitat types. These habitat types have geographical distributions, and hence, our results can be used to identify and prioritize the areas within a region that have a high value for maintaining evolutionary heritage from the Paleogene (Fig. 4). Our approach can be applied to any region where trends in surface area of habitat types, habitat use, and phylogenetic relationships of a major taxon are known. The results of our approach will be most interpretable if in addition, the environmental preferences of species are known.

Existing conservation programs, such as the Habitat Directive implemented by the European Commission (European Commission 2018), do not explicitly protect evolutionary heritage, even though making this heritage a conservation priority has been strongly advocated by many (e.g., Nee & May 1997; Forest et al. 2007; Faith 2015). It is especially worrying that, at least in The Netherlands, habitat types with more recent evolutionary heritage are currently replacing those with much more ancient ones. In The Netherlands, one of the main causes is likely anthropogenic increases of nutrient levels leading to increases in competition. Although recent conservation efforts attempt to protect or partly restore declining habitats locally, the regional deposition of nutrients remains among the highest in Europe (de Heer et al. 2017; Schoukens 2017), and the country is far from the habitat availability of the beginning of the 20th century. If the trends continue, even at reduced pace, there may be no habitats in this region in the future that can support the evolutionary heritage from particular ancient epochs. This alarming situation would have gone unnoticed with the commonly used measures of evolutionary heritage that we tested. Threats to evolutionary heritage from a given epoch may threaten adaptations evolutionary lineages developed to survive the environment of that epoch that have been maintained since then (phylogenetic conservatism [e.g., Prinzing et al. 2001; Wiens & Graham 2005; Wiens 2011]). These are adaptations that may today serve to protect species, and also to protect humans who

Zones of maintenance of evolutionary heritage

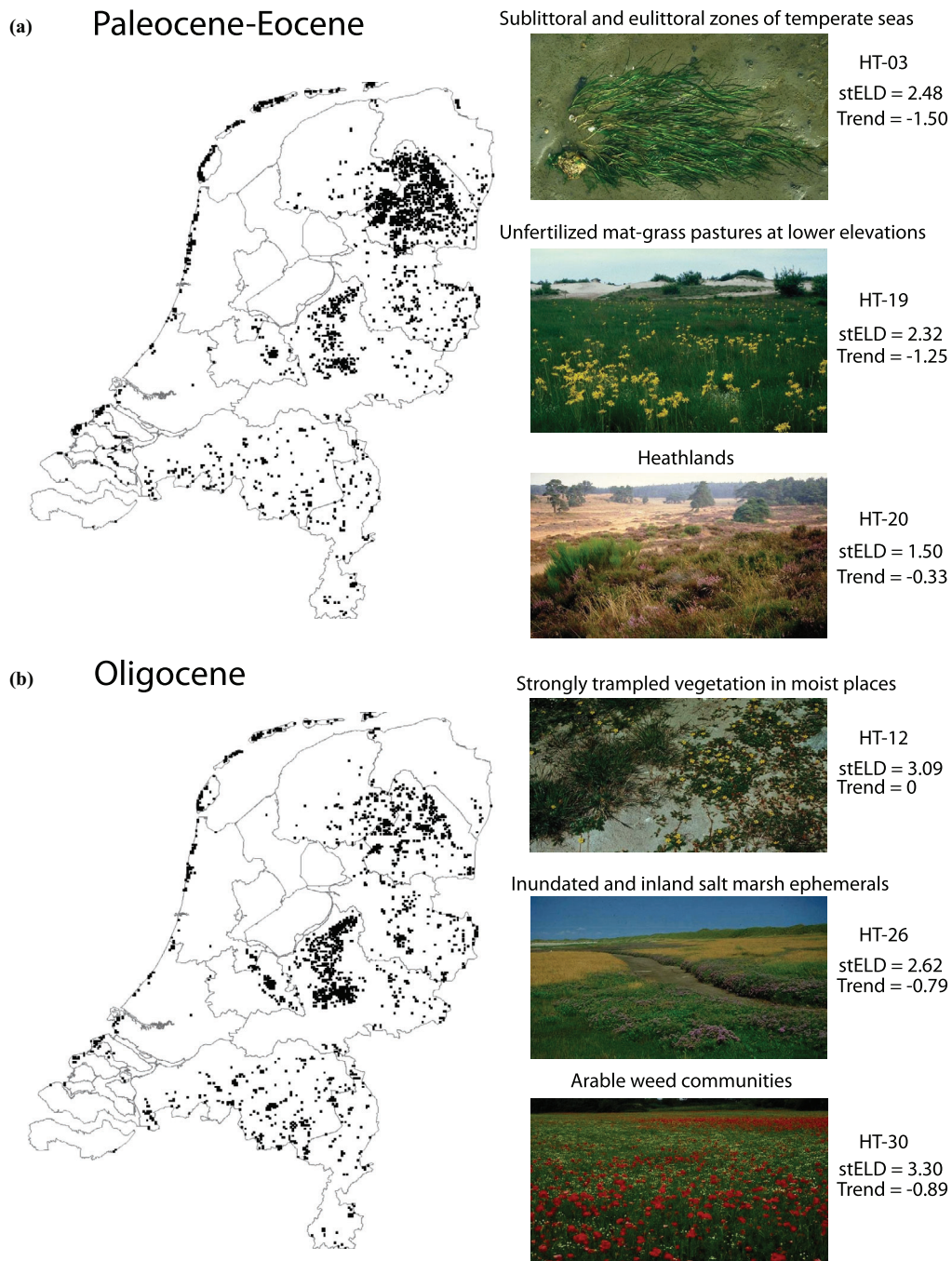


Figure 4. Observations of habitat types with high evolutionary heritage (positive epoch-specific lineage diversity [stELD] values) from the 2 epochs most strongly related to decline of surface area of habitats. Three habitat types with highest epoch-specific lineage diversifications for the (a) Paleocene-Eocene (HT-03,19,20) and (b) Oligocene (HT-12,26,30). Observations are plotted at a resolution of $1 \times 1 \text{ km}^2$ and stem from the national floristic and conservation programs after 2000 and are overall indicative of the true distribution of these habitat types across the country. For descriptions of habitat types, see Supporting Information.

depend on them, from future environmental changes. These changes are often much too rapid to permit de novo evolution of adaptations. Moreover, it is a major ethical problem if humans threaten the evolutionary heritage of an entire epoch of the history of life. This problem may be easier to communicate to the general public than the more abstract loss of phylogenetic branch lengths.

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Supporting Information

Dutch habitat types and species pools with estimates of their trends in the 20th century (Appendix S1), reconstruction of the phylogeny and definition of geological epochs (Appendix S2), details and an illustration of the calculus of stELDs and results per habitat (Appendix S3), commonly used measures of evolutionary heritage of species pools of Dutch habitat types (Appendix S4), inferred environmental conditions in Dutch habitat types (Appendix S5), accounting for multicollinearity and outliers in the data (Appendix S6), proportions of 99 angiosperm families in species pools of Dutch habitat types and selection of families significantly associated with trend (Appendix S7), and results of multiple regression analyses for trend and stELDs based on PU phylogeny of Dutch angiosperms (Appendix S8) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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