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1 **PERSPECTIVE**

2 ***Ecospace: a unified framework for understanding variation in terrestrial***
3 ***biodiversity***

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16 **Abstract.**

17 Understanding patterns in biodiversity is a core ambition in ecological research. Existing ecological
18 theories focusing on individual species, populations, communities, or niches aid in understanding
19 the determinants of biodiversity patterns, yet very few general models for biodiversity have
20 emerged from simplistic approaches. We propose that a systematic, low-dimensional representation
21 of environmental space with building blocks adopted from gradient, niche, metapopulation and
22 assembly theory may unite old and new aspects of biodiversity theory and improve our
23 understanding of variation in terrestrial biodiversity.

24 We propose the term *ecospace* to cover the local conditions and resources underlying diversity.
25 Our definition of ecospace encompasses abiotic *position*, biotic *expansion* and spatiotemporal
26 *continuity*, which all affect the biodiversity of a biotope (α -diversity). *Position* refers to placement
27 along abiotic gradients such as temperature, soil pH and fertility, leading to environmental filtering
28 known from classical community theory. *Expansion* represents the build-up and diversification of
29 organic matter that are not strictly given by position. *Continuity* refers to the spatiotemporal
30 extension of position and expansion.

31 Biodiversity is scale dependent. The contribution of one biotope to large scale diversity must be
32 estimated by considering its unique contribution to the species richness of the surrounding
33 landscape or region or to the biodiversity of the entire planet. In addition to the relationship between
34 ecospace and biotope richness (α -diversity), we also propose a relation between the *uniqueness* of
35 the biotope ecospace and the unique contribution of species to the surrounding larger-scale richness.

36 Whereas the impacts of ecospace position and continuity on biodiversity have been studied in
37 isolation, studies comparing or combining them are rare. Furthermore, biotic expansion has never
38 been fully developed as a determinant of biodiversity, ignoring the megadiverse carbon-depending
39 groups of insects and fungi. Precursors of the ecospace concept have been presented over the last

40 seventy years, but they were never fully developed conceptually for terrestrial biodiversity or
41 applied to prediction of biodiversity.

42 Ecospace unites classical and - at times - contradicting theories such as niche theory, island
43 biogeography theory and a suite of community assembly theories into one framework for further
44 development of a general theory of terrestrial biodiversity.

45

46 **Keywords:** α -diversity; assembly; β -diversity; biotope; community; uniqueness

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48 Introduction

49 Understanding variation in species diversity remains among the major questions facing science
50 in our time (Pennisi 2005). Ecologists have struggled to explain the variation in biodiversity, but
51 only few cross-taxon and cross-habitat theories are widely accepted – perhaps reflecting a classical
52 atomistic focus in biodiversity research on specific selections of species, habitats or processes. As
53 early as 1949, Elton (1949) called for a broader community approach incorporating all types of
54 organisms and their habitats in order to enhance the overall understanding of community assembly
55 and ecosystem function. Similarly, Southwood (1977) realized that no single theory could explain
56 the complex patterns in nature and that theories therefore ought to be pluralistic. Despite great
57 advances in our understanding of the importance of species pools (Zobel 1997, Svenning et al.
58 2015), spatiotemporal continuity (Ovaskainen & Hanski 2001) and ecological gradients (Grace et
59 al. 2016), we are still left with very few generally agreed principles or models explaining variation
60 in biodiversity. Fortunately, molecular techniques now allow us to gather the comprehensive cross-
61 taxon biodiversity data needed for developing this field further (Bohmann et al. 2014, Yoccoz
62 2012). However, a template or framework for understanding and modeling the quantified variability
63 in biodiversity is needed to complement the new techniques.

64 Here, we advocate for a general approach to understand local biodiversity, substituting single
65 species habitat modelling with environmental mapping of both abiotic conditions and organic
66 resources. We suggest ‘ecospace’ – shorthand for ‘ecological space’ – as term for an inclusive
67 framework for biodiversity research and conservation. The basic idea has been outlined in classic
68 works (e.g., Elton 1949, Southwood 1996), but has never been fully developed as a conceptual
69 framework. Meanwhile, the term ‘ecospace’ has developed independently within paleoecology
70 (Bambach 1983) to describe the possible and realized modes and forms of life in prehistoric and
71 modern marine species assemblages (Bambach et al. 2007, Novack-Gottshall 2007).

72 In our reinterpretation of Elton's and Southwood's works, ecospace is defined as the
73 multidimensional and spatiotemporal space of conditions and resources, in which terrestrial
74 biodiversity develops. We define the geospatial basis for ecospace as a biotope, i.e. the physical
75 area, in which a given set of organisms live. The term habitat, in contrast, is used to signify the set
76 of environmental conditions matching the specific needs of a species or a group of species sharing
77 the same niche (Udvardy 1959). Consequently, the ecospace framework can be used to immediately
78 predict variation in α -diversity, and to assess the probable composition of species and, thus, the
79 diversity contribution of a biotope to large-scale biodiversity. In theory, the framework is not
80 limited to a fixed spatial scale, but there are inevitable trade-offs between homogeneity and
81 representation. Ecospace is defined and mapped at biotope scale and represents a spatiotemporal
82 projection of the major physicochemical conditions and realized pools of organic carbon. Every
83 terrestrial biotope - regardless of its ecological setting and spatiotemporal extent - can be described
84 in terms of its ecospace. We presume that the ecospace framework also works in aquatic
85 environments although the spatial delimitation of a given biotope may be less clear and constant
86 because of the continuous flow and mixing of resources, abiotic conditions, biota etc.

87 **Ecospace: the concept**

88 Elton (1949, 1966) did not explicitly mention ecospace, but primordia of the concept are evident
89 in the texts, stating that insect habitats may be defined abiotically, may be formed by host plants or
90 parts of plants, or constitute localized structures, such as dung. Southwood (1978, 1996) explicitly
91 discussed ecospace, but mainly used the concept to signify the physical surfaces livable from the
92 perspective of small-bodied animals like insects. He estimated that the surface area of tree trunks,
93 branches, twigs and foliage of a forest would be about 50-fold the soil surface below the canopy
94 (Southwood 1978), and added that important components of ecospace still were to be included, such
95 as the interior of living or dead plant parts. In this way, both authors briefly addressed the expansion
96 of ecospace by living plants, but also touched upon other components. We take the idea a step
97 further and propose to perceive ecospace as a general measure of the capacity of a given biotope to
98 hold a certain assemblage and richness of species. We define ecospace explicitly for biotopes and
99 with three constituent components: *position*, *expansion* and *continuity* (Fig. 1).

100 Past and present processes shape ecospace and translate ecospace into biodiversity, but ecospace
101 itself is a state of the biotope, not a process. Species pools, from which biotopes are colonized, have
102 been shaped by speciation, extinction, and migration – processes working at large temporal and
103 spatial scales (Belyea & Lancaster 1999). Likewise, small-scale dispersal, colonization, stochastic
104 dynamics and biotic interactions all contribute to populate a given biotope, with its ecospace acting
105 as environmental filters (MacArthur & Wilson 1967, Zobel 1997, Hubbell 2001). A central
106 assumption underlying ecospace as a unified framework for biodiversity research is thus that the
107 ecospace can be mapped independently of the processes shaping the ecospace or populating the
108 biotope, e.g. colonization can be assumed to take place if the ecospace is appropriate in terms of
109 position, expansion and continuity. We do not attempt to cover variation in biodiversity between
110 continents or biogeographical regions under influence of large-scale historical effects.

111 **Ecospace – its basic elements and spatial extent**

112 *Position*

113 Ecospace position reflects the position of the biotope in a (hyper-)space spanned by multiple
114 abiotic gradients (Fig. 1). Position is the combination of biotope values for a number of continuous
115 abiotic gradients, such as soil pH, nutrient availability, soil texture, soil moisture and temperature
116 (e.g. Ellenberg et al. 1991) (Fig. 2). Homogeneity within the biotope is a prerequisite for a
117 meaningful measurement of ecospace position represented by a set of common biotope values for
118 abiotic condition. For some abiotic variables, e.g. temperature or soil moisture, extremes or
119 temporal variation may be more relevant to define a position than the mean. Ecospace position
120 resembles the abiotic niche but seen and mapped from the habitat perspective rather than the species
121 perspective. We assume that a simple ecospace defined by a few abiotic factors may adequately
122 predict species composition and significant parts of species richness (Dray et al. 2012). Position
123 determines the abiotic filtering from a larger species pool (van der Valk 1981, Zobel 1997, Wilson
124 1999) (Fig. 2), the size of which in turn depends on factors such as evolutionary history and
125 historical bottlenecks (Bennett & Provan 2008, Jansson & Davies 2008, Eiserhardt et al. 2015). In
126 Europe for example, high vascular plant species richness in alkaline soils has been proposed to
127 reflect favorable conditions in evolutionary centres within floristic regions (Pärtel 2002), coupled
128 with the putative extinction of more acidophilous species during Pleistocene glacial maxima (Ewald
129 2003). Although ecospace defines the filtering of the species pool and not its formation it has been
130 suggested that local-scale processes driven by variation in ecospace position may even have had a
131 feedback relation to the buildup of the regional species pool (Bruun & Ejrnæs 2006), indicating a
132 possible non-random link between position and species pool. Change in ecospace position can be
133 caused by natural disturbances or succession as well as land-use change. Ecospace position may
134 also feedback on processes, e.g. some positions are more likely to attract grazing or uprooting

135 mammals (e.g. Bailey et al. 1996), some are more prone to wildfires (Cardille et al. 2001), some
136 intensify asymmetric resource competition between plants (Schwinning & Weiner 1998) and some
137 may induce certain trophic interactions (Chase 1996). However, most natural processes are entirely
138 or partly decoupled from the abiotic part of ecospace. For example coastal erosion, herbivory,
139 trampling, defecation, flooding and strong winds may all take place across a wide range of different
140 biotopes.

141 *Expansion*

142 The second component of ecospace is defined as the accumulation, formation and diversification
143 of organic structures and substrates for species to live on and from (Figs 1 and 2). Expansion
144 consists of pools and structures of organic matter, ultimately derived from the autotrophic biota, and
145 provides food, shelter and space for other species (Fig. 3). Consequently, expansion includes both
146 the accumulation and spatial distribution of biomass (structural complexity of vegetation) and the
147 partitioning of biomass into functionally separated carbon pools and structures (diversification of
148 organic matter). Plant species richness, foliage, flowers (providing nectar and pollen), fruits/seeds,
149 tree trunks, branches, dead wood, litter, carcasses and dung, all contribute to the expansion of
150 ecospace providing substrates that heterotrophic animals and fungi can live on or from (Figs 1 and
151 3). While any biotope may be characterized by a quantified position along major abiotic gradients,
152 expansion rather works by increasing the opportunities for species in the biotope. Certain elements
153 of expansion may provide habitat for numerous species, for example c. 30% of the pollen-collecting
154 bee species of Central and Northern Europe only collect pollen from a single plant genus
155 (Pekkarinen 1997), 728 species of phytophagous insects are associated with *Salix* and 699 species
156 with *Quercus* in Germany (Brändle & Brandl 2001), and more than 1500 species of saproxylic
157 fungi are reported from Finnish forests (Siitonen 2001). While expansion may take place in
158 response to the conditions given by ecospace position it can also be decoupled from position (e.g.

159 pollen and nectar, coarse woody debris, dung and carcasses may occur almost independently of
160 position, Fig. 3). Expansion is highly dynamic and challenging to quantify and predict compared to
161 position, as some carbon pools – e.g. floral resources, dung or carcasses – are ephemeral, that is,
162 they are hard to predict in space and time.

163 Elton (1966) acknowledged the importance of structure and organic resources provided by other
164 organisms for the capacity of a biotope to support diversity. Although we use other terms, we agree
165 that the diversity of resources provided by other organisms is a strong and often overlooked
166 determinant of potential biodiversity. Each additional carbon pool and structure expands ecospace
167 by adding new habitats and resources and potential α -diversity therefore increases with expansion.
168 Expansion may be criticized for being impossible to quantify given the countless number of
169 possible organic resources. We argue, however, that a limited number of parameters may
170 adequately represent ecospace expansion, e.g., number of different plant species, variety of plant
171 life forms, and availability of flowers, litter, dead wood and dung.

172 *Continuity*

173 Continuity refers to the extension in time and space of a given ecospace position and expansion
174 (Fig. 1). Spatial and temporal continuity are estimated with respect to the biotope in question, but
175 are measured for the surrounding area (spatial) and the conditions preceding (temporal) the current
176 ecospace. Spatial and temporal continuity affect the colonization of a biotope (cf. meta-community
177 theory, Leibold et al. 2004). Continuity in ecospace position enhances the probability of
178 colonization and establishment of species from the species pool and decreases the risk of local
179 extinction. We suggest a strict definition of temporal continuity per se, excluding the habitat
180 formation time needed to develop e.g. veteran trees, charred coarse woody debris and diversity of
181 carbon pools in the soil (Fretwell 1977, 1987, Nordén et al. 2014). With increasing continuity the
182 realized species richness in the biotope approaches the potential species richness constrained by the

183 regional species pool and the available conditions and resources.

184 Disruption of temporal continuity may happen due to major successional changes or abrupt
185 disturbance. Disruption of continuity causes a change in ecospace position and/or expansion e.g.
186 with wildfires, coastal erosion or land use change. For example cultivation for forestry or
187 agriculture will disrupt the continuity of a natural level of expansion in a semi-natural grassland or
188 old growth forest. Even if the abiotic position remains constant, the cultivation of crops enforces
189 structurally uniform and species-poor vegetation (Whitehouse 2006). However, change in
190 disturbance regimes in naturally disturbed areas will also lead to a loss of continuity (Kodric-Brown
191 & Brown 2007). In this case, recurrent disturbance may be needed in order to maintain a given
192 position and expansion (e.g. strong wind and sand transportation in white dunes, flooding in river
193 beds, herbivory and trampling in grasslands).

194 **Large scale diversity: the uniqueness of ecospace**

195 Given that ecospace can predict species composition, the contribution of a biotope to β -diversity
196 (Tuomisto 2010) can be predicted by its uniqueness in position, expansion and continuity in the
197 context of a larger geographic area (Fig. 1). Uniqueness is not part of the formulation of ecospace
198 but should be regarded as an extrapolation of ecospace that enables us to assess the contribution of
199 the biotope to the biodiversity of the surrounding landscape. Rare positions in ecospace will
200 contribute more than common positions to the hypervolume of ecospace positions along a
201 predefined number of gradients, and consequently may be an indicator of compositional turnover
202 (β -diversity). Unlike position, organic carbon resources cannot be characterized by a mean value,
203 but either take a binomial value (present-absent) or an abundance value (mass, cover, frequency).
204 Therefore, expansion will contribute to uniqueness by the diversity of realized carbon pools. Similar
205 to positions, carbon pools may be weighted by their rarity, so that rare pools such as coarse woody
206 debris or species- and flower-rich biotopes count more than common pools. Different species

207 groups may respond differently to ecospace variation, but we hypothesize that biotopes having
208 unique positions and expansions in ecospace generally hold more unique species and thus
209 contribute more to β -diversity at a landscape scale (Fig. 1). For this reason, even types of ecospace
210 with limited expansion or representing positions with small associated species pools may contribute
211 significantly to the total biodiversity if they represent rare positions or rare expansions, as can be
212 recorded in e.g. raised bogs, sparsely vegetated sand dunes or biotopes with large carcasses. Spatial
213 continuity and the uniqueness of an ecospace are related so that high spatial continuity normally
214 implies low uniqueness of ecospace among neighbor biotopes. However, the two elements are not
215 reciprocal. For example, a regionally rare biotope may have high local continuity – e.g. old growth
216 forest patches in a national park. Similarly, a locally discontinuous biotope such as a woodland lot
217 in an agricultural landscape may be regionally common.

218 **Vertical organization of ecospace**

219 Ecospace may be seen as vertically organized in a trophic hierarchy where biodiversity generally
220 accumulates from the bottom to the top, with important positive top-down feedbacks (Fig. 2). At the
221 bottom, we find the abiotic position providing resources and conditions for primary producers
222 constituting the second level. At this level diversity will be determined by the abiotic environmental
223 sorting of species from the regional species pool under influence by interspecific competition and
224 temporal continuity (Belyea & Lancaster 1999). The plants expand ecospace by forming the living
225 and dead organic carbon pools and biotic surfaces underpinning the megadiverse groups of
226 heterotrophic organisms, i.e. animals and fungi (DeAngelis 1992). Further expansion takes place in
227 response to biotic interactions. Herbivores, especially large herbivores, contribute by partial
228 destruction of plant tissue (Bakker et al. 2015), transformation and relocation of plant litter and
229 provision of dung, live animals and carcasses as resources for predators, parasites and decomposers.

230 To fully understand the link between ecospace and biodiversity, several – ideally all – species
231 groups must be studied, because diversity patterns based exclusively on the sampling of one
232 taxonomic group may differ markedly from other groups within the same biotope (white bars
233 indicating species richness for different taxonomic groups in Fig. 1). Different aspects of ecospace
234 are more important for some species groups than for others. Thus, limiting analyses to well-known
235 or easily sampled taxonomic groups may blur important biodiversity patterns.

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237 **Applications, perspectives and caveats**

238 According to classical niche theory (Hutchinson 1957), every species can be described by its
239 fundamental niche: the hypervolume comprising all states of the environment allowing the species
240 to exist. From a theoretical point of view, biodiversity could be studied and managed by considering
241 the sum of all species' niches. In practice, however, the classic approach is intractable, even for
242 small and relatively species-poor areas, because it requires estimation of niche parameters for all
243 species in the species pool and interaction coefficients for all pairs of species. While the ecospace
244 concept is compatible with the niche concept, it has a different scope. The ecospace concept refers
245 to possible combinations of important ecological parameters without direct reference to limiting
246 conditions or to interspecific competition (Bambach et al. 2007). Despite the obvious advances to
247 be gained in studies of relationships between selected taxonomic groups and simple underlying
248 gradients (e.g. Grace et al. 2016 for productivity and plant richness), a unifying multi-taxon
249 approach to describe and fully understand the variation in biodiversity is needed. The justification
250 for ecospace as a new framework for studying variation in biodiversity lies in its conceptualization
251 of all major aspects of a biotope needed to understand its capacity to support populations of species.
252 Ecospace includes the role of abiotic gradients, biotic resources and spatiotemporal continuity.
253 Thus, it opens for an integration and comparison of e.g. environmental filtering and biotic
254 interactions along environmental gradients (Keddy 1992, Kraft et al. 2008) and neutral processes
255 according to the rules of island biogeography (MacArthur & Wilson 1967, Hubbell 2001). On top
256 of these points, we add expansion as the build-up and diversification of pools of organic carbon
257 providing an essential niche-space for megadiverse taxonomic groups such as arthropods and fungi.
258 Despite the obvious contribution of these taxa to terrestrial biodiversity, they are rarely covered
259 extensively in biodiversity studies, mainly because they are too difficult to identify and too resource
260 demanding to record. This situation may change in the near future given the rapid development of

261 metagenomics (Coissac et al. 2016). We acknowledge the scale-dependency of biodiversity (Levin
262 1992, Collwell & Coddington 1994) by suggesting uniqueness as a biotope-scale metric for the
263 contribution of the biotope to the biodiversity of the total landscape in which it is situated.
264 Uniqueness is not itself part of ecospace, but rather meant as a link from ecospace driven variation
265 in α -diversity and biotic composition to β - and γ -diversity – particularly important in conservation
266 planning (Brooks et al. 2006). But also, and perhaps more importantly, the ecospace approach urges
267 researchers to search for the simplest possible explanatory model of variation in biodiversity,
268 pruning away all redundant or inferior variables. We recommend taking the full model as starting
269 point and reducing this in a search for maximum parsimony.

270 We have deliberately defined ecospace to describe a measurable state and excluded processes
271 such as disturbance and succession. This makes a difference to approaches using processes to
272 predict variation in species richness or composition, e.g. the intermediate disturbance hypothesis
273 (Grime 1973) or the disturbance axis in the CSR-classification of plant strategies (Grime 1977).
274 This said, we would very much encourage research in the biological processes required to fill, clear,
275 change, expand or share a given ecospace.

276 In the palaeoecological community, a similar concept of ecospace has been developed and
277 advanced, in which ecospace signifies the potential and realized modes of life for a prehistoric
278 marine fauna (Bambach 1983, Bambach et al. 2007). While emphasis is on the mapping of life
279 modes as proxy for ecospace filling, the basic idea is fully compatible, namely that resource
280 availability and abiotic conditions in the ecosystem constrains the possible modes of life, and also
281 that diversity begets diversity, just as is the case with biotic expansion (Bambach et al. 2007).

282 Ecospace may also be applied as concept in nature conservation. At the biotope scale, managers
283 can consider ways to promote ecospace expansion or to restore a more natural ecospace position.
284 Likewise, conservation planning can target spatiotemporal continuity in prioritized localization of

285 protected areas within landscapes. Ideally, managers can map elements of ecospace without full
286 biotic inventories reducing costs without sacrificing meaningful conservation targets. Ecospace may
287 also be useful as evaluation metric in open-ended management, where the target cannot be specified
288 in terms of a particular set of species. Current conservation management almost invariably targets
289 conspicuous or easily mapped groups of species, such as mammals, plants and birds (EU Birds
290 Directive 1979, EU Habitats Directive 1992, Ricketts et al. 1999), despite the fact that fungi and
291 insects constitute the vast majority of species richness.

292 We are well aware that the value of ecospace as a framework for ecological research and nature
293 conservation can only be assessed by extensive testing against comprehensive empirical data. We
294 therefore invite fellow scientists and conservationists to join us in testing and revising the concept
295 and to contribute to the research in ecospace, underlying drivers, and the resulting biodiversity.

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432 alternative explanation of species coexistence? *Trends in Ecology & Evolution*, 12, 266-269.

433 **Fig. 1.** Ecospace mapped empirically for four contrasted biotopes in Denmark, showing how
434 biotopes may vary independently in position, expansion, continuity and uniqueness; and how that
435 affects α -diversity. Red: arable field, yellow: dry, old-growth forest, green: swamp forest, blue:
436 lichen-rich dune.

437 Position is represented here by two important abiotic gradients: soil moisture (% volumetric water
438 content) and nutrients (% leaf P). Expansion is represented by build-up of different carbon sources:
439 i.e. flower density (range=0-70/m²), number of vascular plant species (No. plants; range=0-60),
440 canopy height (range=0-8 m), litter mass (range=0-150 g) and coarse woody debris (CWD;
441 range=0-50 m³). Continuity is divided into spatial (% cover of the ecospace type within 500 m) and
442 temporal continuity of the biotope (years since last major environmental change). The ecospace
443 (position, expansion and continuity) effect on α -diversity is illustrated by the white bars on the
444 photos representing the number of species found (divided into arthropods (right), plants (middle)
445 and fungi (left)). Uniqueness is an estimate of the 'rarity' of the biotope at a larger scale estimated
446 by $1/\log(\% \text{ national cover of ecospace type})$ of the given biotope. The higher the uniqueness, the
447 more the biotope is expected to contribute to β -diversity, here represented by the number of red-
448 listed species found in the four biotopes (red numbers). Photos: Lars Skipper.

449 **Fig. 2.** Biotope ecospace is vertically organized along a trophic axis with biodiversity
450 accumulating from the bottom to the top. At the bottom abiotic position provides resources and
451 conditions for plant growth. First, plants expand ecospace, then herbivores and decomposers
452 contribute to further expansion (diversification of organic carbon) and provide resources for
453 zooparasites and predators. Regional species pools are filtered according to biotope position and
454 dependence on lower trophic levels. Local dispersal, community assembly processes including
455 biotic interactions affect the link between ecospace and local biodiversity in the biotope and also
456 have a feedback effect on the regional species pool.

457 **Fig. 3.** Examples of biotic expansion by various carbon sources: Upper left: Plants as food
458 source for herbivores, the specialist moth *Zygaena filipendulae* (Linnaeus, 1758) feeding on *Lotus*
459 *corniculatus* (Linnaeus, 1758). Upper right: Flowers as a pollen and nectar source for the oligolectic
460 solitary bee *Andrena hattorfiana* (Fabricius, 1775), feeding exclusively on *Knautia arvensis* (L.)
461 Coult flowers. Middle left: Biotrophic interactions by three different fungus species forming
462 ectomycorrhizae with roots of a deciduous tree. Middle right: The stump of a beaver-cut birch as
463 habitat for the bracket fungus *Trametes versicolor* (Lloyd, 1921). Lower left: Dung as food source
464 for the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758). Lower right: Carcasses as food source for
465 a vulture, *Necrosyrtes monachus* (Temminck, 1823). Photo credits: Rasmus Ejrnæs (*Zygaena*), Jens
466 H. Petersen (mycorrhiza), Thomas Borup Svendsen (*Trametes*), Morten DD Hansen (*Andrena*,
467 *Typhaeus*), Rune Sø Neergaard (*Necrosyrtes*).

Figure 1
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150 100 50 0 No. species

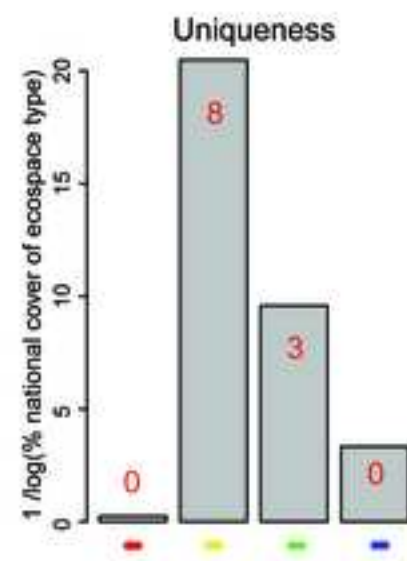
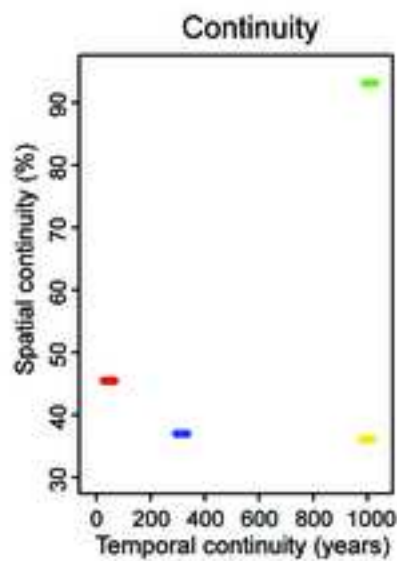
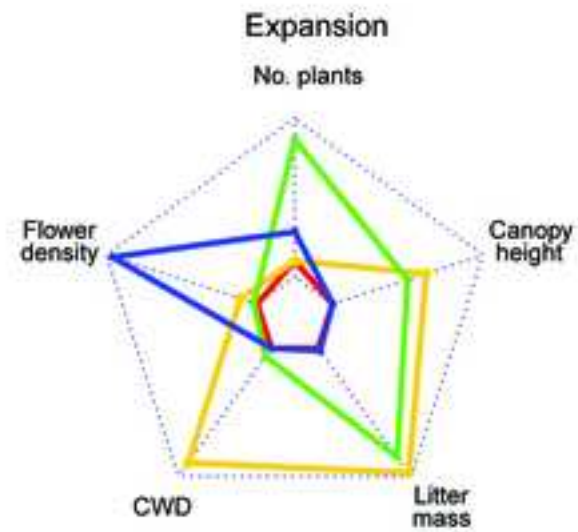
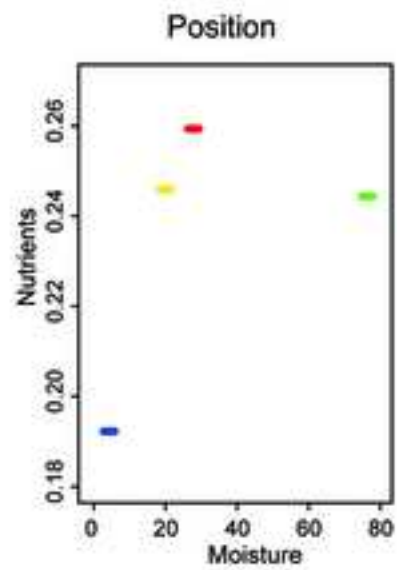
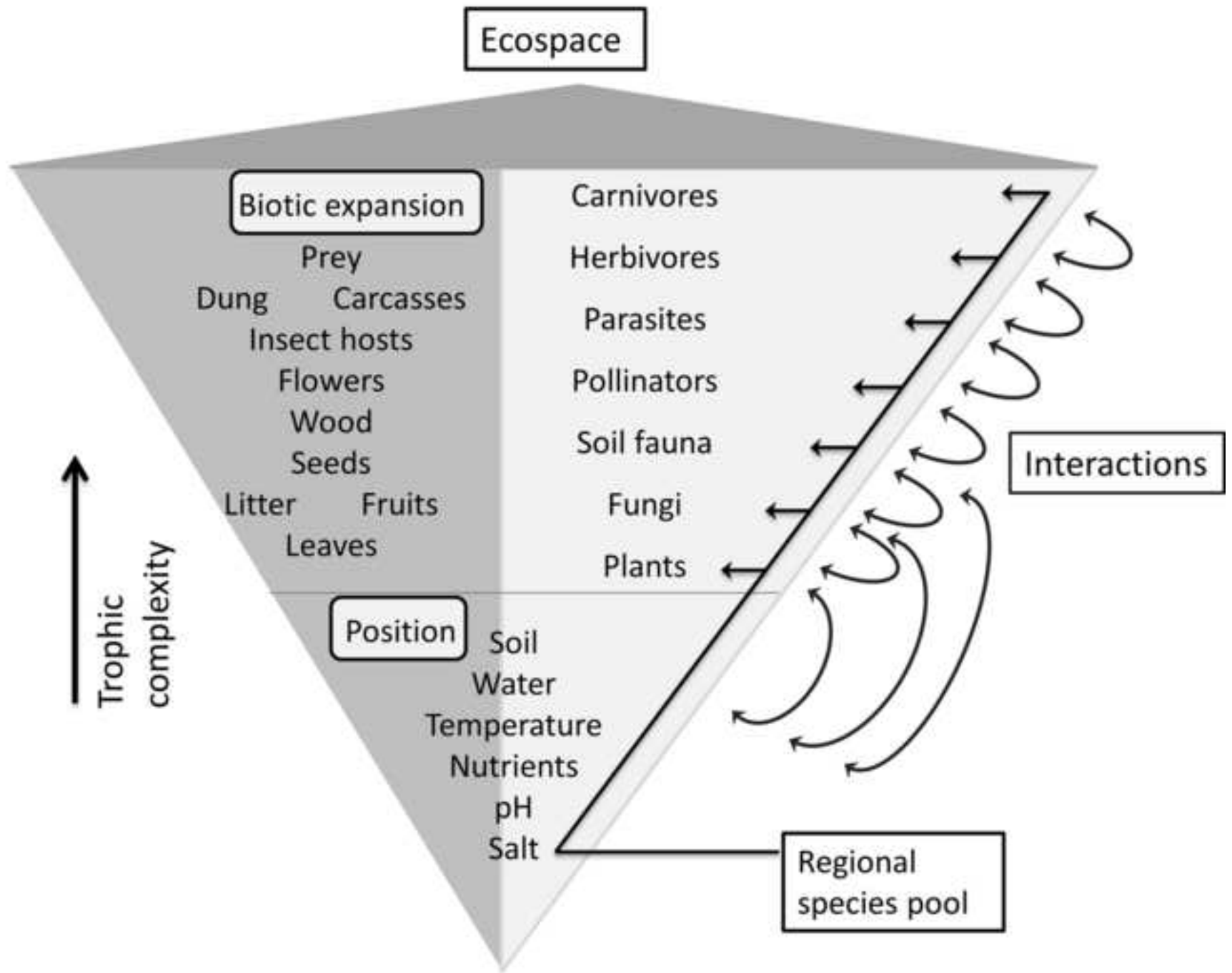
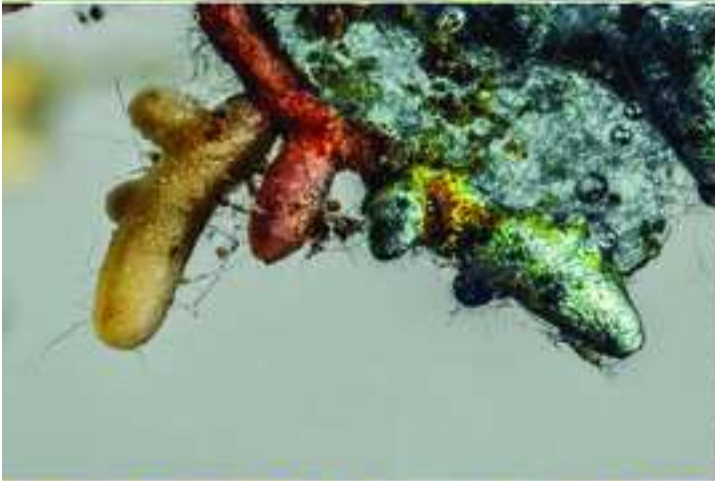


Figure 2
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Zusammenfassung

Die Muster der Biodiversität zu verstehen ist ein zentrales Anliegen der ökologischen Forschung. Ökologische Theorien, die auf einzelne Arten, Populationen, Gemeinschaften oder Nischen zielen, helfen dabei, aber nur sehr wenige generelle Modelle zur Biodiversität sind aus einfachen Ansätzen hervorgegangen. Wir schlagen vor, dass eine systematische Darstellung des Umweltraumes mit wenigen Dimensionen, die Bausteine aus der Gradienten-, Nischen-, Metapopulations- und Gemeinschaftstheorie verwendet, alte und neue Aspekte der Biodiversitätstheorie vereinigen und unser Verständnis zur Variation terrestrischer Biodiversität verbessern könnte. Wir schlagen den Begriff '*ecospace*' vor, um die lokalen Bedingungen und Ressourcen, die der Diversität zugrunde liegen, abzudecken. Diese Definition von '*ecospace*' umfasst die abiotische '*position*', die biotische '*expansion*' und die raumzeitliche '*continuity*', die alle die Biodiversität (α -Diversität) eines Biotops beeinflussen.

'*Position*' bezieht sich auf die Lage entlang von abiotischen Gradienten (Temperatur, Boden-pH, Fruchtbarkeit), woraus sich eine Wirkung als Umweltfilter aus der klassischen Gemeinschaftstheorie ergibt. '*Expansion*' beschreibt den Aufbau und die Diversifizierung organischer Substanz, die nicht durch die '*position*' vorgegeben sind. '*Continuity*' beschreibt die raumzeitliche Ausdehnung von '*position*' und '*expansion*'. Biodiversität ist skalenabhängig. Der Beitrag eines Biotops zur großräumigen Diversität muss bestimmt werden, indem sein besonderer Beitrag zum Artenreichtum der umgebenden Landschaft, der Region oder des Planeten berücksichtigt wird. Zusätzlich zur Beziehung zwischen '*ecospace*' und Artenreichtum eines Biotops (α -Diversität), schlagen wir auch eine Beziehung zwischen der '*uniqueness*' des '*ecospace*' eines Biotops und seinem besonderen Beitrag an Arten zum großräumigen Artenreichtum vor. Während die Einflüsse von '*position*' und '*continuity*' auf die Biodiversität einzeln untersucht wurden, sind Studien, die sie vergleichen oder kombinieren, selten. Darüber hinaus ist biotische '*expansion*' niemals vollständig als bestimmender Faktor für die Biodiversität

ausgearbeitet worden, wobei die megadiversen heterotrophen Gruppen der Insekten und Pilze ignoriert wurden. Vorläufer des 'ecospace'-Konzepts hat es in den letzten 70 Jahren gegeben, aber sie wurden nie vollständig für die terrestrische Biodiversität entwickelt oder zur Vorhersage von Biodiversität eingesetzt. Das 'ecospace'-Konzept vereinigt klassische und zuweilen einander widersprechende Theorien wie Nischentheorie, Theorie der Inselbiogeographie und eine Reihe von Theorien zur Gemeinschaftsbildung in einem Beziehungsgefüge zur weiteren Entwicklung einer allgemeinen Theorie der terrestrischen Biodiversität.

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