



## Short communication

# High and balanced contribution of regional biodiversity hotspots to epiphytic and epixylic lichen species diversity in Great Britain

Jeňýk Hofmeister<sup>a,b,\*</sup>, Jan Vondrák<sup>c,d</sup>, Christopher Ellis<sup>e</sup>, Brian Coppins<sup>e</sup>, Neil Sanderson<sup>f</sup>, Jiří Malíček<sup>c</sup>, Zdeněk Palice<sup>c</sup>, Andy Acton<sup>g</sup>, Stanislav Svoboda<sup>c</sup>, Rhiannon Gloor<sup>a</sup>

<sup>a</sup> Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Suchbát, 165 00 Praha 6, Czech Republic

<sup>b</sup> Department of Biogeochemical and Hydrological Cycles, Global Change Research Institute, The Czech Academy of Sciences, Bělidla 986/4a, 603 00 Brno, Czech Republic

<sup>c</sup> Institute of Botany, The Czech Academy of Sciences, Zámek 1, CZ-252 43 Příhonice, Czech Republic

<sup>d</sup> Faculty of Science, University of South Bohemia, Branišovská 1760, CZ-370 05 České Budějovice, Czech Republic

<sup>e</sup> Royal Botanic Garden Edinburgh, Arboretum Pl, Edinburgh EH3 5NZ, UK

<sup>f</sup> Independent Researcher, Southampton, UK

<sup>g</sup> Independent Researcher, Taynult, UK



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## ABSTRACT

We surveyed epiphytic and epixylic lichens in eleven 1-hectare forest plots located in representative old-forest stands in four distinct regions of Great Britain that are well-known centres of lichen biodiversity. We aimed to analyse the patterns of lichen biodiversity in these important biodiversity hotspots from a British perspective. In total, we recorded 550 lichen species in 11 ha, i.e. 73% of the presently known British epiphytic and epixylic lichen flora. Species richness per site was regionally stratified and varied from 126 to 235 species. Although the presence of frequent species coincided with total species richness in the respective hotspot, rare species (those with <50 records in Great Britain since 2000) were more balanced among hotspots and relatively independent of species richness. Species turnover contributed significantly and evenly to the species composition regardless of species richness so that hotspots did not have nested structure, typical for the hotspots in Central Europe. Although British hotspots generally shared more species within regions than between regions, geographic distances between regions did not correspond with the differences in species composition. The results document the importance and irreplaceability of the surveyed hotspots for lichen diversity in Great Britain, notwithstanding their current species richness and past depletion due to long-term acid deposition and habitat degradation.

## 1. Introduction

Spatial patterns of species richness over regions is connected mainly with the richness of common species (Lennon et al., 2004). A higher contribution of rare species tends to be concentrated in geographically-limited areas with a higher abundance of specialist species (Clavel et al., 2011). The number of small-ranged species increased in the last decades due to ongoing human exploitation and landscape homogenization (Howard et al., 2020). A contraction of geographic ranges makes species prone to extinction, particularly with regard to anticipated climate change (Román-Palacios and Wiens, 2020). For effective biodiversity conservation, it is necessary to identify and then protect areas with a

cumulative occurrence of rare species; this is simplified when communities of rare species of several different taxa occupy the same areas and habitats (Hofmeister et al., 2019). However, the spatial distribution of rare and threatened species is often scattered in different areas and habitats, even within a single taxonomic group (Orme et al., 2005).

In the traditionally-inhabited European landscape, rare epiphytic and epixylic lichens are concentrated in habitats less influenced by forest management, habitat degradation and fragmentation, and areas with low air pollution (Hauck et al., 2013). For example, epiphytic lichens in Central Europe consist of only a subset of the species that are maintained in a few preserved hotspots with limited areas of hundreds or even tens of hectares (Hofmeister et al., 2016; Malíček et al., 2018,

\* Corresponding author at: Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, Suchbát, 165 00 Praha 6, Czech Republic

E-mail address: [hofmeisterj@fld.czu.cz](mailto:hofmeisterj@fld.czu.cz) (J. Hofmeister).

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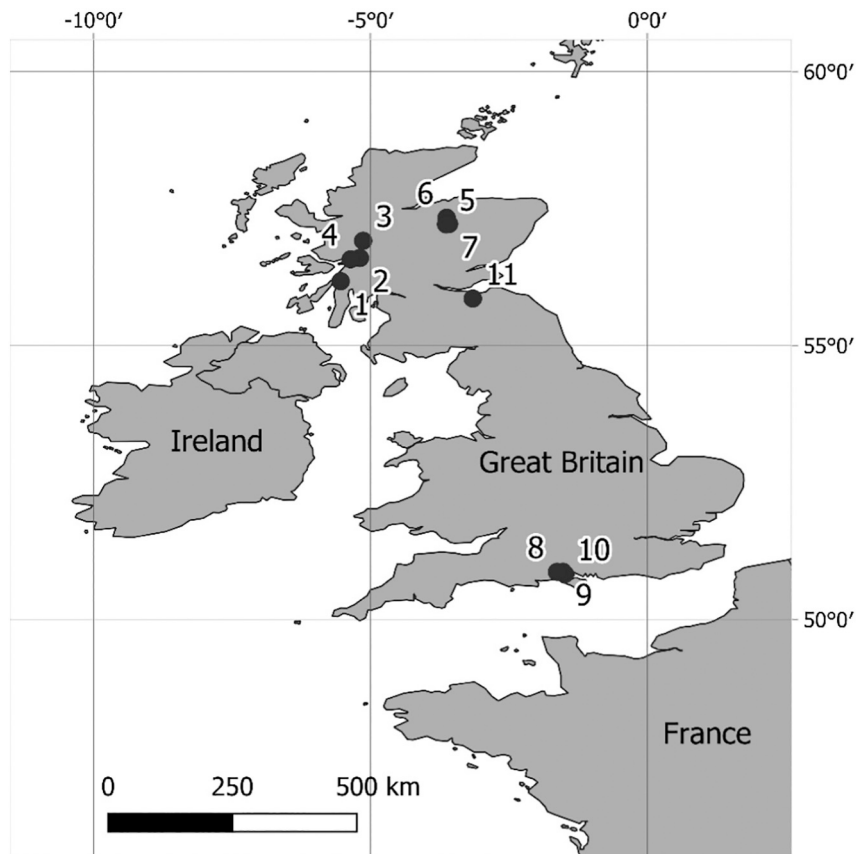


Fig. 1. Locations of the eleven studied hotspots in Great Britain; description of the sites is in Table S1.

2019). Consequently, regional differences in species composition are controlled mainly by nestedness components of beta-diversity (Baselga, 2010), while species turnover is redundant over the broader landscape (Hofmeister et al., 2016; Malčec et al., 2019).

Great Britain has one of the world's best surveyed lichen floras (Smith et al., 2009). Large numbers of field records are held in the British Lichen Society Database, making it possible to obtain rather precise information about regional species lists. Due to this long-term research effort, we know that the harmful effects of deforestation and air pollution on epiphytic lichen communities in Great Britain, particularly in southern England, are among Europe's highest (Ellis et al., 2011).

In this study, we surveyed epiphytic and epixylic lichen communities in 11 hotspots distributed in four regions of Great Britain that are well known for extraordinarily high lichen biodiversity. Three sampled regions had multiple hotspots, in landscapes with locally-extensive old-growth woodland. Their origins lie predominately in traditional land use methods (e.g. extensive grazing by stock and game), but they have more checkered recent histories ranging from unchanged, incorporated into 19th century forestry use and subsequently abandoned, or being relative recently incorporated into non-intervention stands. The fourth, in south-eastern Scotland, is in a more highly-anthropogenic landscape (Ellis and Coppins, 2007). Based on the results, we aim to evaluate the contribution of i) regional hotspots to total species diversity ii) frequent and rare species to the overall species richness, and iii) turnover and nestedness components of beta-diversity to regional differences in species composition across Great Britain.

## 2. Methods

Epiphytic and epixylic lichen hotspots were selected within well-preserved forest stands in four British regions with high lichen

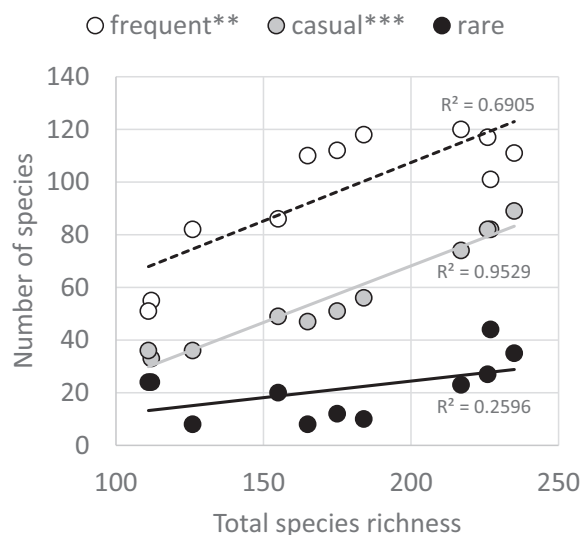
diversity and variable climatic conditions: Scottish western coast with euoceanic climate (four plots), Scottish inland with rather continental climate (three plots), English New Forest with oceanic warm temperate climate (three plots), and a suburban area of Edinburgh, Scotland (one plot) (Fig. 1).

All forest stands correspond to 'ancient woodland' as defined by the UK's Ancient Woodland Inventory (Roberts et al., 1992; Spencer and Kirby, 1992); they are semi-natural woodlands that have existed continuously in the landscape since at least the mid-18th Century (Scotland: Roberts et al., 1992; Walker and Kirby, 1987) or the 17th Century (England: Spencer and Kirby, 1992), and presumably much longer, except for the birch-dominated site in Nethy Bridge which appears long-established with possible origins in the 19th Century.

Square 1-hectare plots were placed in structurally-diverse forest habitats (Appendix 1; Table S1) to meet criteria for local biodiversity hotspots according to the methodology designed for exploration of lichen biodiversity hotspots (Vondrák et al., 2018): (1) presence of a multi-layered canopy indicating a non-even-aged forests, (2) presence of over-mature, dying and dead trees with rough bark partly covered by mosses, (3) presence of both standing and lying dead wood, (4) assumption of the highest species diversity at the local scale based on preliminary survey, (5) the presence of small natural forest gaps, and (6) possibility to include canopy lichens (e.g. accessibility of the tree canopy, presence of fresh windthrows or at least fallen big branches with canopy lichens). Surveys were performed between June and December 2018 by at least three of seven expert lichenologists (for details see authorship) with a survey time of 6.5–10 h per site. The species records were complemented by three-class abundance estimates and the list of substrates (Table S2). Voucher specimens were collected for most of the recorded species and were deposited in Edinburgh – E (BC, CE), Průhonice - PRA (JV, ZP) and in the personal herbaria of AA, JM, NS. Numerous specimens, especially sterile crusts, were identified through

**Table 1**  
Species richness and composition of epiphytic and epixylic lichen communities in the hotspots.

Site	Species richness	Number of				Mean Sørensen dissimilarity
		Unique species	Rare species	Casual species	Frequent species	
1) Eilean	217	11	23	74	120	0.5305
2) Glen Creran	235	19	35	89	111	0.5260
3) Glen Loy	227	20	44	82	101	0.5227
4) Glen Stockdale	226	18	27	82	117	0.5449
5) Nethy Bridge - birch	112	11	24	33	55	0.6174
6) Nethy Bridge - pine	155	13	20	49	86	0.5459
7) Nethy Bridge - mixed	111	12	24	36	51	0.6549
8) New Forest beech	184	15	10	56	118	0.5363
9) New Forest holly	165	11	8	47	110	0.5347
10) New Forest oak	175	11	12	51	112	0.5294
11) Rosslin	126	13	8	36	82	0.5767



**Fig. 2.** Linear regression between total species richness and number of frequent, casual and rare species, respectively, in eleven studied hotspots of epiphytic and epixylic lichens in Great Britain. For each regression, the coefficient of determination ( $R^2$ ) and symbol of significance at the level  $p < 0.001$  (\*\*\*),  $p < 0.01$  (\*\*) or  $p < 0.05$  (\*) are displayed.

thin layer chromatography (TLC). Some specimens were sequenced for nuclear ITS and/or mitochondrial SSU DNA barcode and identified by the standard nucleotide BLAST search.

We evaluated contributions of frequent, casual and rare epiphytic and epixylic lichen species at the plots from the perspective of Great Britain using all lichen species records since 2000 extracted from the British Lichen Society Database. We considered species frequent as those with >500 records, casual as species with 50 to 500 records, and rare as species with <50 records. We assessed changes in lichen species composition with geographic distance using Sørensen dissimilarity index as a measure of total beta-diversity (Baselga, 2010). Additionally, we computed two components of beta-diversity: i) Simpson dissimilarity which represents species composition turnover and ii) the remnant part of dissimilarity accounted for nestedness. Analyses were performed in R Development Core Team (2013), using the package 'betapart' (Baselga et al., 2015).

### 3. Results

Species richness in eleven 1-hectare plots differed considerably, ranging from 111 to 235 epiphytic and epixylic lichens (Table 1). In total, we recorded 550 lichen species; 73% of the known British lichen epiphytes (Table S2). Almost one-third of all recorded species (154) occurred in only one site and had a higher relative contribution in

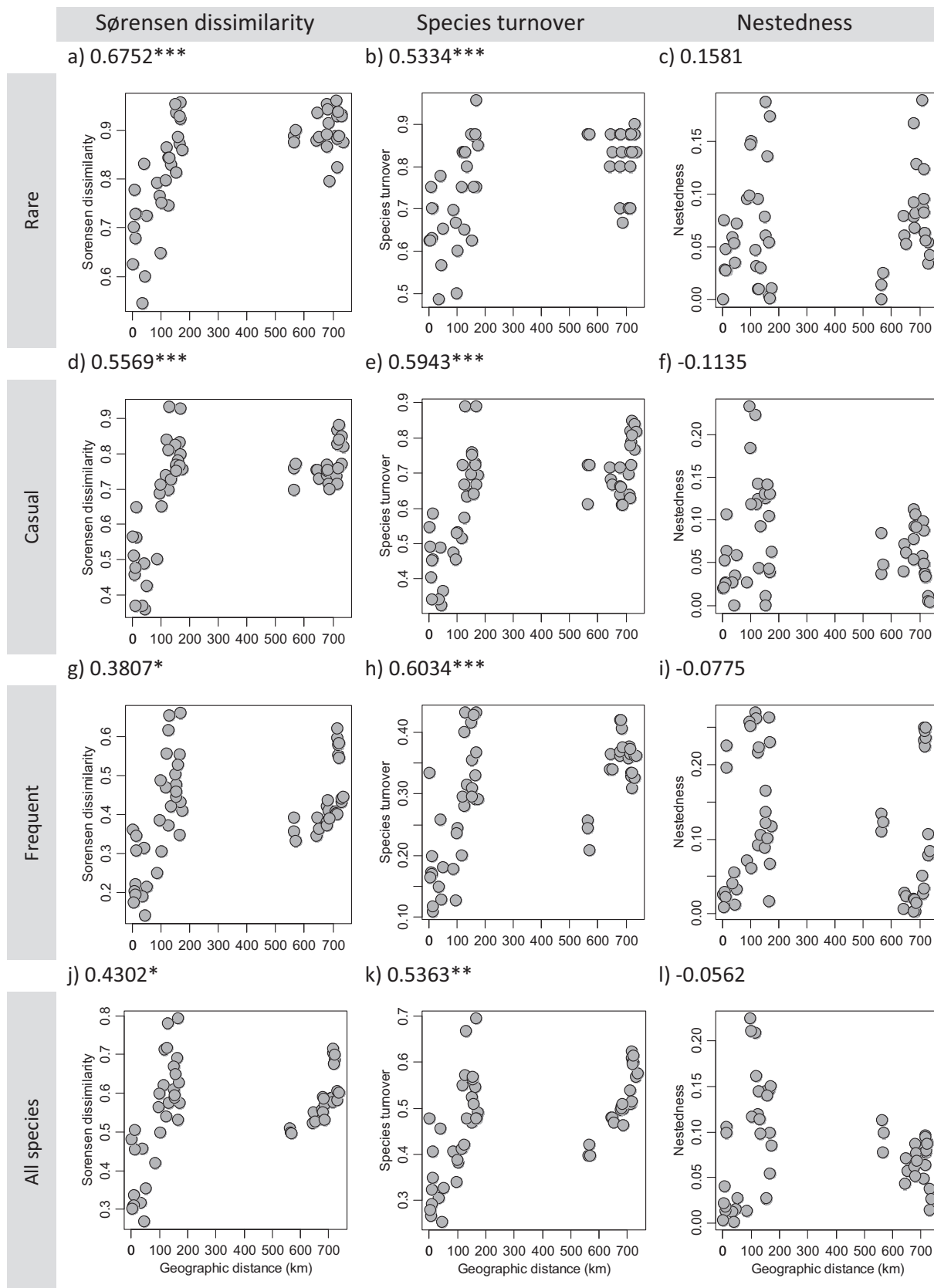
species-poor sites (Table 1). Total species richness coincided with the number of frequent and casual species ( $p < 0.05$ ) in the respective sites while only weakly with the number of rare species ( $p > 0.05$ , Fig. 2).

Species dissimilarity in lichen communities increased with the distance of sites up to approximately 100 km but remained high and relatively uniform for all pairs of sites with a distance above 100 km (Fig. 3). This pattern was unrelated to species rarity, but differences in species composition increased from frequent to rare species. When we decomposed species dissimilarity to its turnover and nestedness components, it revealed that processes underlying dissimilarity in lichen communities consisted almost exclusively of species turnover while nestedness contributed negligibly.

### 4. Discussion

The decisive role of commonness for species richness seems to be a general rule governing local species richness of many taxa in various regions (Lennon et al., 2004; van Schalkwyk et al., 2019). Rare species might reflect overall species richness patterns if we accounted for their proportion in species richness (Heegaard et al., 2013). This pattern fits the spatial distribution of epiphytic lichens in traditionally-inhabited and highly-polluted regions in Western and Central Europe (Hauck et al., 2013; Hofmeister et al., 2016; Malíček et al., 2019). Central European epiphytic lichen communities have a strong nested structure dependent on species richness in which infrequent and rare species only occupy sites with a complete set of widespread generalists (Malíček et al., 2018; Vondrák et al., 2015). In Central Europe, the proportion of beta-diversity allocated to the turnover component is especially low for macrolichens and other desiccation-sensitive lichens (Bässler et al., 2016).

British epiphytic and epixylic lichen communities have also been impoverished by high industrial pollution and ancient woodland fragmentation and degradation (Ellis et al., 2011). Accordingly, here, total species richness was lower in hotspots located in small and isolated fragments of ancient forests in more industrial regions. However, in contrast with studies from Central Europe, the proportion of rare species was balanced along the richness gradient. Each hotspot comprised of 5 to 11% of species that were not recorded at another site, which, unexpectedly, peaked in species-poor sites. Since lichen species associations were relatively balanced between tree species in our study (Table S3), the observed differences in tree species composition should not simply explain the higher contribution of rare species in species-poor sites. These results convincingly document the irreplaceability of particular hotspots for total species richness in Great Britain, despite regional differences in past species impoverishment. It does not imply that preserving a small number of pre-eminent forest habitats is sufficient for conserving current lichen diversity. The unique species composition in particular hotspots makes a large part of the current lichen diversity highly prone to extinction that might be delayed for more than a century after habitat degradation (Johansson et al., 2013a, 2013b). This risk is



**Fig. 3.** Dissimilarity in species composition partitioned to components of species turnover (Simpson dissimilarity) and nestedness for rare, casual, frequent and total epiphytic and epixylic lichen species recorded in eleven hotspots in Great Britain. The symbol \*\*\* indicates significance at the level  $p < 0.001$ , \*\*  $p < 0.01$  and \*  $p < 0.05$ .

further accentuated by ongoing climate change, with more adverse effects expected in continental than oceanic climatic zones (Ellis, 2015).

The extent to which hotspots within a given region host a unique set of species raises the challenge of understanding the scale necessary for effective dispersal (colonisation) among sites. While lichens can effectively disperse over landscapes (Anstett et al., 2013), seriously constrained colonisation ability has been confirmed for many species at the local- and landscape-scale (Bartels and Chen, 2012). Species with narrow niches and large propagules - which usually represent rare species - are often more dispersal-limited (Johansson et al., 2012).

#### 4.1. Conservation implications

The contribution of regional hotspots to total epiphytic and epixylic British lichen diversity was high and unexpectedly equal, notwithstanding probable differences in long-term human impact. However, this positive result might gradually diminish due to extinction debt in the case of small, isolated hotspots. Hence, effective conservation of rare species needs i) to protect current lichen diversity hotspots and ii) active support for the regeneration of other potentially suitable old-forest habitats across the British landscape.

Our findings document the potential importance and uniqueness of regional biodiversity hotspots, even though they are isolated in the long-term inhabited landscape. It seems that some communities can - at least partly and temporary - resist species extinction and associated species homogenization. Although we cannot offer any reliable explanation based in ecological theory for this evidence yet, this is a challenge encouraging further detection and protection of all more preserved habitats within cultural landscapes, including those overlooked due to low total species richness.

#### CRediT authorship contribution statement

JH and JV developed the theoretical framework of the study, performed data analyses and wrote the manuscript. The contribution of the two first authors is equal. All authors (except for JH and RG) collected field data. CE and BC provided critical feedback that helped shape the research and the final draft. BC extracted data from British Lichen Society Database.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109443>.

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