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## Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S6

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References (36–50)

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# Evolutionary Conservation of Species' Roles in Food Webs

Daniel B. Stouffer,<sup>1,2</sup> Marta Sales-Pardo,<sup>3</sup> M. Irmak Sirer,<sup>4</sup> Jordi Bascompte<sup>1</sup>

Studies of ecological networks (the web of interactions between species in a community) demonstrate an intricate link between a community's structure and its long-term viability. It remains unclear, however, how much a community's persistence depends on the identities of the species present, or how much the role played by each species varies as a function of the community in which it is found. We measured species' roles by studying how species are embedded within the overall network and the subsequent dynamic implications. Using data from 32 empirical food webs, we find that species' roles and dynamic importance are inherent species attributes and can be extrapolated across communities on the basis of taxonomic classification alone. Our results illustrate the variability of roles across species and communities and the relative importance of distinct species groups when attempting to conserve ecological communities.

Present-day ecosystems face threats, such as climate change and invasive species, that permeate entire communities (1). Partly for this reason, ecology has moved toward more holistic approaches that consider all species in an ecosystem and the network of interactions between them (2). This network approach has led to a greater understanding of the structural properties of ecological systems (3) and the community-wide consequences of empirically observed network structure (4, 5). A drawback of this community focus is that the interplay between individual species and community-level dynamics has largely been ignored (6, 7). Because conservation ef-

forts are generally focused on species, this problem has precluded a deeper assessment of the conservation implications of network theory (1).

Here we focus on the species level, to understand the generality of species' roles and their dynamic importance when embedded in their community's network. The prevailing notion is that the ecological role of a species in a network is a direct result of its interactions with other species (8–10), in particular the prey it consumes and the predators that consume it. However, given structural definitions of species' roles, it is often unclear how to extrapolate from a species' structural role to its dynamic relevance. With this in mind, we introduce here a definition of species' roles based around the concept of "network motifs" (11).

Any network can be decomposed into a set of smaller subnetworks which, when reassembled, form the original network. Depending on the type of network studied, particular subnetworks ap-

pear more frequently than would be expected at random and represent fundamental building blocks: These are referred to as network motifs (11). Crucially, the number and type of motifs that make up a food web are known to directly affect the web's stability and persistence (12–16). In ecological networks, motifs provide a meso-scale characterization of community structure by quantifying how collections of three species come together to form a larger community (17, 18). Here, we take network motifs one step further to better highlight the behavior of their most basic component: the individual species.

By definition, any motif of size  $n$  is composed of  $n$  species; for reasons of symmetry, however, each species does not necessarily appear in a unique position (Fig. 1). As an illustrative example, consider the two unique motifs made up of two species:  $A \rightarrow B$  and  $A \leftrightarrow B$  (19). In the first motif, the positions of  $A$  and  $B$  are not equivalent, because they allow us to distinguish between the two species. On the other hand, the positions of  $A$  and  $B$  are indistinguishable in the second motif. This implies that, formally, a motif of  $n$  species can have anywhere from 1 to  $n$  unique positions. If we consider three-species combinations, we find that there are 13 unique motifs composed of 30 unique positions (20, 21) (fig. S1).

We examined the motif pattern of all species from 32 empirical food webs that describe which predator-prey interactions are observed in the community (21) (table S1). These food webs come from a variety of different environments, encompassing marine, terrestrial, freshwater, and estuarine habitats. To quantify the roles of all species in a food web, we directly enumerate, across all motifs, the frequency  $c_{ij}$  that species  $i$  appears in each position  $j$ . Therefore, in each network, the motif profile of any species  $i$  is provided by its vector  $\vec{c}_i = \{c_{i1}, c_{i2}, \dots, c_{i29}, c_{i30}\}$ .

<sup>1</sup>Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), calle Américo Vespucio sin número, 41092 Sevilla, Spain. <sup>2</sup>School of Biological Sciences, University of Canterbury, Christchurch 8140, New Zealand. <sup>3</sup>Departament d'Enginyeria Química, Universitat Rovira i Virgili, 43007 Tarragona, Spain. <sup>4</sup>Department of Chemical and Biological Engineering, Northwestern University, Evanston, IL, 60208, USA.

To better refine our definition of a species' role, we search for sets of species that exhibit statistically similar motif profiles. The resulting motif profile–based grouping of species provides the complete set of unique, empirically observed roles. Species with more interactions will appear in more motifs and will therefore be characterized by larger values of  $c_{ij}$ . To take this into account, we use a network-based method that identifies groups while explicitly controlling for the total number of motifs each species participates in (21–23) (figs. S2 and S3). In spirit, our methodology is akin to identifying sets of species that have similar normalized motif profiles  $\vec{f}_i = \{f_{i1}, f_{i2}, \dots, f_{i29}, f_{i30}\}$ , where  $f_{ij} = c_{ij} / \sum_k c_{ik}$ , and the sum is across all positions (24). Because the sum gives the total number of times that species  $i$  appears in all of the motif positions,  $f_{ij}$  corresponds to the relative frequency that species  $i$  appears in position  $j$  (Fig. 2). Because our analysis controls for a species' total number of interactions, it provides an unbiased measure of the topological configuration of a species' interactions.

Now that we have a means to quantify species' roles, the next step is to extend our structural measure to its dynamic consequences. Simulations show that we can associate a “benefit”  $s_j$  to each position  $j$  across all motifs, determined by how much community persistence increases or decreases when a single motif  $j$  is added to the network (16). Because each position in a single motif appears with the same overall frequency, we necessarily assume that all positions from the same motif have the same associated benefit. Given the benefit of each position and our species-specific motif profiles, we can calculate

a species' expected mean effect on community persistence. Mathematically, this is given by

$$b_i = \sum_j^{\text{positions}} f_{ij} s_j \quad (1)$$

where  $b_i$  is the benefit of species  $i$  in terms of its effect on community persistence (25). Here, the benefit of each species provides an assessment of the degree to which each species in a community is a keystone species (26). A keystone species is one whose presence is particularly critical for a community's biodiversity maintenance, as compared to all other species present (27). Our analysis, therefore, allows us to quantify the complete gradient across which species contribute to the organization and dynamics of their network.

Across the 2468 empirical species and 32 webs, we observe 54 distinct empirical roles (table S1). At the network level, we find that some of the 32 webs contain species from just two distinct roles, whereas others contain species from up to 22 distinct roles (mean  $7.4 \pm 5.4$ ). Intriguingly, the diversity of roles found in a food web is neither directly proportional to the amount of species diversity ( $P = 0.63$ ) nor the amount of taxonomic diversity ( $P = 0.82$ ) found within the community.

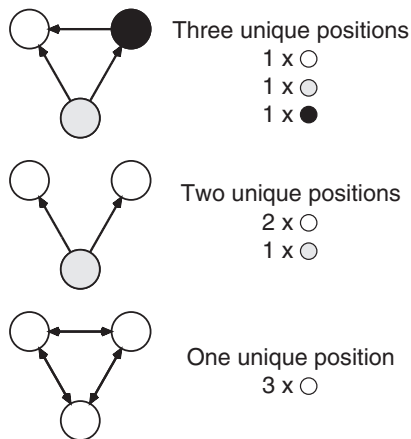
The majority of roles consist exclusively of intermediate species (46 out of the 54 roles), whereas the remaining roles are made up of either (i) basal and intermediate species or (ii) intermediate species and top predators. Roles, however, are not distributed proportionally across trophic levels; the 1026 basal, 991 intermediate, and 451 top species in the data are assigned to one of four, 53, or five roles, respectively. The interaction patterns of basal species and top predators therefore appear to be particularly constrained when they are part of a larger community. In addition, the diversity of roles played by intermediate species paints a more complex picture than the usual top-down versus bottom-up approach (28).

Building on the strong variability in roles across species and communities, we next aim to

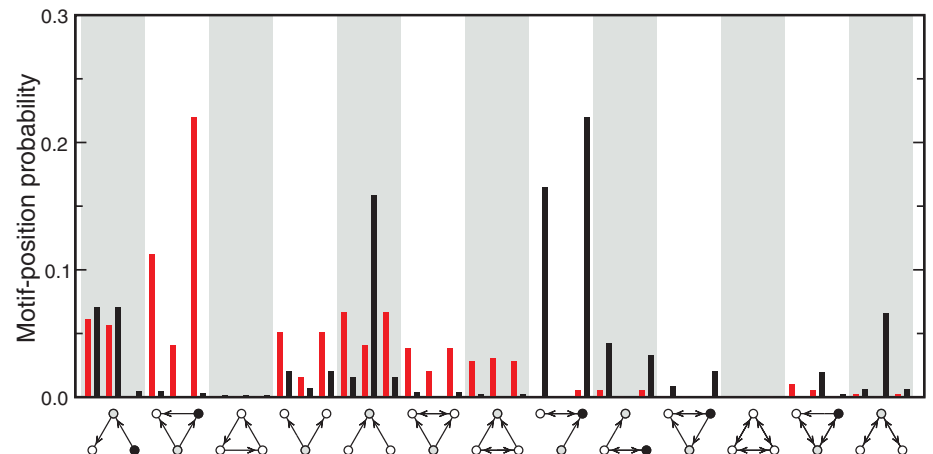
determine the extent to which a species' role is evolutionarily conserved. A strong tendency would help to predict the role of species in a new network; for example, after introduction or invasion. We find that species with the same role have a significant tendency to be homogenous both in terms of phylogenetic similarity and dynamic importance (21) (Fig. 3). In fact, we observe a large degree of phylogenetic signal in how species are embedded in their network and their subsequent dynamic importance (table S2). First, closely related species have a significant tendency to have similar motif profiles in a significant fraction of empirical webs (13 out of the 18 webs for which we have taxonomic data,  $P < 10^{-4}$ ). Second, closely related species also have a significant tendency to be of similar benefit to their home community than would be expected at random (15 out of 18 webs,  $P < 10^{-4}$ ). This relationship holds while controlling for the fact that phylogenetically related species also tend to have similar trophic positions (21, 29).

Phylogenetic signal, as we have measured it here, is quantified at the scale of an individual community. We wish, however, to see if this result reflects an intrinsic property of each species and thus can be extrapolated across distinct communities composed of different species. To do so, we take advantage of specific details regarding our empirical data. Ten of the empirical webs come from third- or fourth-order tributaries of the same river in New Zealand (30). We compare the relative importance of the 150 species (out of 192 total) that occur in at least 2 of the 10 different networks. We find that, if a species is dynamically important in one web, it shows a significant tendency to be important in the other webs in which it appears, and vice versa (21).

To some degree, however, this result may be a direct consequence of (i) within-community phylogenetic signal and (ii) insufficient community variability between the 10 webs. Indeed, though the webs differ somewhat in the degree to which the adjacent land had been developed for pasture



**Fig. 1.** Uniqueness of positions in three-species motifs. We show 3 of the 13 unique three-species motifs. Each circle represents a different species, and interacting species are connected by an arrow that goes from prey to predator. Although each motif consists of three species, not every position is unique for reasons of symmetry. From top to bottom, these motifs are made up of three, two, and one unique positions, respectively. In each motif, the different unique positions are shown in different colors (black, white, or gray).



**Fig. 2.** Species differ in their tendency to appear in distinct motif positions. We show the species-specific motif profiles  $\vec{f}_i$  for two different species from the empirical webs (red and black bars, respectively). The height of each bar is equal to the probability  $f_{ij}$  that the species appears in the position found immediately below.

(30), there is substantial overlap between them in terms of species composition. Given observed patterns of evolutionary conservation of ecological interactions (31–33), we cannot exclude the possibility that similarities in species composition across the 10 New Zealand webs are sufficient to

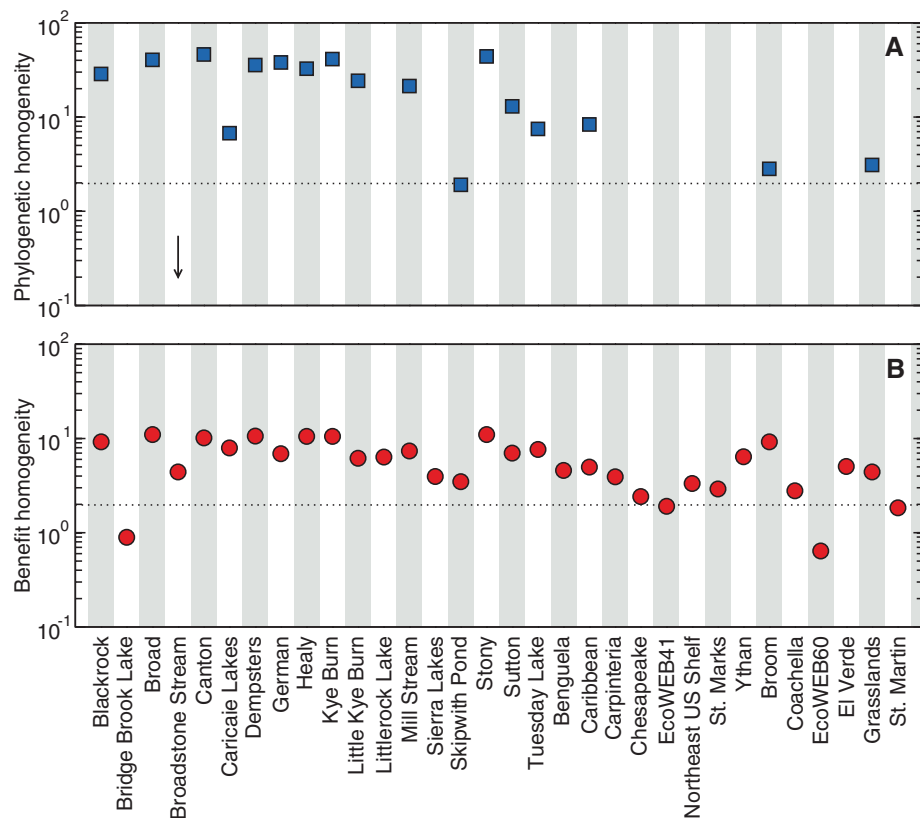
account for the observed similarities in species' dynamic importance.

A stronger and more conclusive test of the generality of our results would be to compare species across the complete set of food webs, in which there is far greater variability of commu-

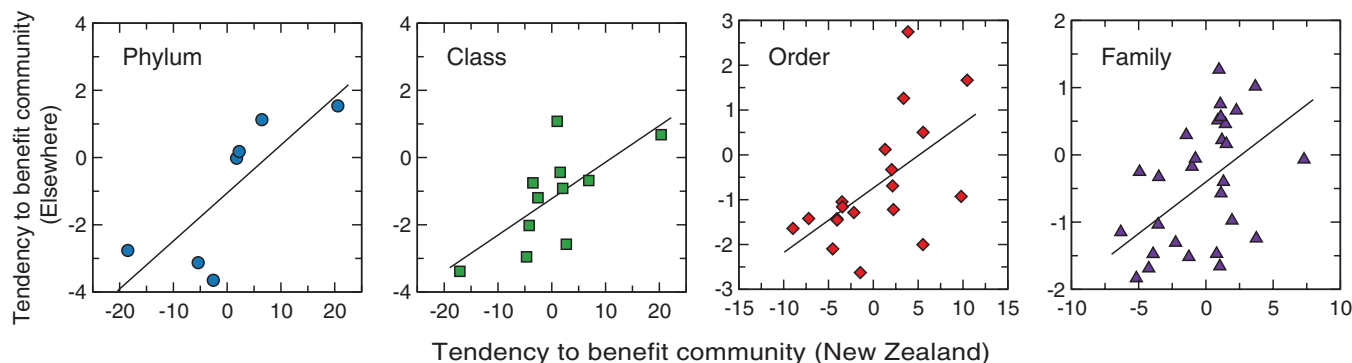
nity composition. At the species level, we cannot extend this analysis to the other food webs, because none of the 192 species found in the New Zealand food webs appears elsewhere. Nevertheless, we can make comparisons at coarser levels of taxonomic aggregation. For example, we can compute the tendency of a given phylum of species to be important in the New Zealand webs and compare this to the tendency for the same phylum appearing in webs outside of New Zealand. Across all phyla, significant correlation could indicate that intrinsic factors are a stronger determinant of species' dynamic importance than are the properties of the community in which they occur.

In our comparative analysis, we find that dynamically important phyla in New Zealand also tend to be dynamically important elsewhere, and vice versa ( $P = 0.036$ ; Fig. 4 and table S3). Moreover, we observe significant correlation at the class, order, and family levels ( $P = 0.018$ ,  $P = 0.012$ , and  $P = 0.005$ , respectively). This implies that there are particular taxonomic groups of species that are expected to play an important dynamic role independent of the specifics of their particular ecological community. It therefore appears that species dynamic importance—the degree to which a species acts as a keystone species—may indeed be an intrinsic and inherent species attribute that arises as a consequence of species' evolutionary histories.

Our study of species' roles and their dynamic consequences has important implications about how best to decide which conservation actions will most successfully preserve ecological communities (1), linking species-specific variability to overall network persistence. The number and type of roles observed in a community do not increase systematically with increasing species or taxonomic diversity. This means that actions that focus on maintaining overall levels of biodiversity may not be sufficient to preserve an ecosystem's long-term viability. On the other hand, the dynamic implications of species' roles provide a potential starting point when deciding



**Fig. 3.** Species' roles capture important components of the variability observed across species in a network. **(A)** Species' roles are phylogenetically homogeneous; that is, they have a significant tendency to be closely related phylogenetically. **(B)** Species' roles also tend to be homogeneous in terms of their dynamic importance to their community. Here, values of phylogenetic or benefit homogeneity close to zero indicate no tendency; in contrast, values greater than 2 (dotted line) indicate significant similarity within species' roles. We have ordered the webs so that the first 18 are from freshwater environments, the next 8 from marine environments, and the last 6 from terrestrial environments. The arrow in (A) indicates an observed value that is less than the y-axis minimum of  $10^{-1}$ .



**Fig. 4.** Species dynamic importance is conserved across diverse ecological communities. We calculate whether specific groups of species are observed to benefit their home community as a result of their motif profiles. Values greater than 2 indicate a significant tendency to positively influence community persistence, whereas values less than  $-2$  indicate a significant tendency to negatively

influence community persistence. We repeat this analysis for every phylum, class, order, and family for which species appear both in the New Zealand webs and in the others. At each of these levels of classification, we observe significant correlation between species' tendencies to benefit their community ( $P < 0.05$ ), irrespective of the community context in which they occur.



which species should receive priority in conservation efforts: those from groups that make the strongest contributions to the community persistence. Perhaps most importantly, our results indicate that this predictive power spans a broad range of taxonomic scales.

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19. Here an arrow ( $\rightarrow$ ) indicates an interaction in the direction of mass and energy flow, from prey to predator.
20. We focus on three-species motifs because they provide both significant information content and reduced overall complexity (there are 199 and 9364 unique motifs composed of four and five species, respectively).
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24. All results reported here hold if we choose to focus on species' absolute motif profiles  $c_i$  instead of normalized motif profiles.
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## Supporting Online Material

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SOM Text

Figs. S1 to S3

Tables S1 to S3

References (34–65)

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# Plant UVR8 Photoreceptor Senses UV-B by Tryptophan-Mediated Disruption of Cross-Dimer Salt Bridges

John M. Christie,<sup>1,2</sup> Andrew S. Arvai,<sup>2</sup> Katherine J. Baxter,<sup>1\*</sup> Monika Heilmann,<sup>1\*</sup> Ashley J. Pratt,<sup>2</sup> Andrew O'Hara,<sup>1</sup> Sharon M. Kelly,<sup>1</sup> Michael Hothorn,<sup>3†</sup> Brian O. Smith,<sup>1</sup> Kenichi Hitomi,<sup>2,4,5</sup> Gareth I. Jenkins,<sup>1‡</sup> Elizabeth D. Getzoff<sup>2‡</sup>

The recently identified plant photoreceptor UVR8 (UV RESISTANCE LOCUS 8) triggers regulatory changes in gene expression in response to ultraviolet-B (UV-B) light through an unknown mechanism. Here, crystallographic and solution structures of the UVR8 homodimer, together with mutagenesis and far-UV circular dichroism spectroscopy, reveal its mechanisms for UV-B perception and signal transduction.  $\beta$ -propeller subunits form a remarkable, tryptophan-dominated, dimer interface stitched together by a complex salt-bridge network. Salt-bridging arginines flank the excitonically coupled cross-dimer tryptophan "pyramid" responsible for UV-B sensing. Photoreception reversibly disrupts salt bridges, triggering dimer dissociation and signal initiation. Mutation of a single tryptophan to phenylalanine retunes the photoreceptor to detect UV-C wavelengths. Our analyses establish how UVR8 functions as a photoreceptor without a prosthetic chromophore to promote plant development and survival in sunlight.

UVR8 (UV RESISTANCE LOCUS 8) orchestrates the expression of more than 100 genes in *Arabidopsis* in response to ultraviolet B (UV-B) wavelengths (280 to 315 nm) (1–4). The *uvr8* mutant exhibits UV-B sensitivity from decreased expression of genes conferring UV protection (1, 5). UV-B exposure promotes both rapid UVR8 accumulation in the nucleus (6), where the protein binds chromatin via histones (1, 7), and interaction with COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1) to initiate transcriptional responses (3, 8). In plant

extracts and in heterologous systems, UV-B exposure triggers UVR8 dimer dissociation to initiate signaling (9). Tryptophan has been implicated in UV-B perception (4, 9), but the absence of detailed three-dimensional information on dimer assembly precludes understanding of the mechanisms for UVR8 photoreception and signaling.

To investigate UVR8 structure/function relationships, we made recombinant *Arabidopsis* UVR8 (10) for biophysical analyses (figs. S1 and S2). Purified UVR8 (fig. S2A) is a homodimer that dissociates into monomers after exposure to

narrowband, long-wavelength UV-B (fig. S2B); the dose-response relationship (fig. S2C) mirrors UVR8 behavior in plant extracts (9). Moreover, UV-B–induced monomerization is reversible; the active, dimeric photoreceptor spontaneously reassembles within hours in vitro and again responds to UV-B (Fig. 1A). UVR8 absorbs strongly at 280 nm (fig. S3), as expected from its complement of aromatic residues (14 Trp, 10 Tyr, and 8 Phe per 440-residue monomer). Photoactive, purified UVR8 lacks any bound cofactor, demonstrating that reversible UV-B–induced dimer dissociation is a property intrinsic to the protein.

The x-ray crystallographic structure of UVR8 (Fig. 1) was determined to 1.7 Å resolution (table S1) by molecular replacement with the RCC1 (Regulator of Chromosome Condensation 1) domain of E3 ligase HERC2 as the probe (10). UVR8 has a seven-bladed  $\beta$ -propeller fold, like

<sup>1</sup>Institute of Molecular, Cell and Systems Biology, College of Medical, Veterinary and Life Sciences, Bower Building, University of Glasgow, Glasgow G12 8QQ, UK. <sup>2</sup>Department of Molecular Biology and Skaggs Institute for Chemical Biology, The Scripps Research Institute, La Jolla, CA 92037, USA. <sup>3</sup>Plant Biology Laboratory, The Salk Institute for Biological Studies, La Jolla, CA 92037, USA. <sup>4</sup>Life Science Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA. <sup>5</sup>Section of Laboratory Equipment, National Institute of Biomedical Innovation, 7-6-8, Saito-Asagi, Ibaraki, Osaka 567-0085, Japan.

\*These authors contributed equally to this work.

†Present address: Structural Plant Biology Laboratory, Friedrich Miescher Laboratory of the Max Planck Society, Tuebingen, Germany.

‡In whose labs this research was jointly undertaken and to whom correspondence should be addressed. E-mail: gareth.jenkins@glasgow.ac.uk (G.I.); edg@scripps.edu (E.D.G.)

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