

The extent of functional redundancy changes as species' roles shift in different environments

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Assessing the ecological impacts of environmental change requires knowledge of the relationship between biodiversity and ecosystem functioning. The exact nature of this relationship can differ considerably between ecosystems, with consequences for the efficacy of species diversity as a buffer against environmental change. Using a microbial model system, we show that the relationship can vary depending on environmental conditions. Shapes suggesting functional redundancy in one environment can change, suggesting functional differences in another environment. We find that this change is due to shifting species roles and interactions. Species that are functionally redundant in one environment may become pivotal in another. Thus, caution is advised in drawing conclusions about functional redundancy based on a single environmental situation. It also implies that species richness is important because it provides a pool of species with potentially relevant traits. These species may turn out to be essential performers or partners in new interspecific interactions after environmental change. Therefore, our results challenge the generality of functional redundancy.

biodiversity–ecosystem functioning | functional redundancy | environmental change | microbial model system | species interactions

Many ecosystems are currently in decline due to rapid loss of biodiversity and immense changes in species compositions (1). The impact of these changes on important ecosystem processes is still unclear (2, 3). Ecosystem functioning (e.g., in terms of biomass production) is often positively correlated with species richness (4–8). This correlation is typically explained by two types of mechanisms that are not mutually exclusive: selection and complementarity (9, 10). The former refers to the rising probability for species with particular traits (e.g., highly productive or resource-efficient species) to be included and achieve high abundance in species-rich communities. The latter refers to the rising potential for particular processes to operate in species-rich communities, such as niche partitioning (e.g., species use different resources or exploit limiting resources in different ways) or positive interactions (e.g., a species facilitates growth of another species). Complementarity can thus lead to species-rich communities performing better than any of the included species in monoculture (transgressive overyielding) (11, 12). As a consequence of these mechanisms, the biodiversity–ecosystem functioning (BEF) relationship is affected by the number and identities of species, their evenness within the community, their functional traits, and their interactions (13–17).

The BEF relationship also reflects whether species are functionally redundant and perform similar roles in given communities. Functioning increasing with species richness points to functional differences among the species (i.e., the added species have unique roles for ecosystem functioning). Saturation in functioning points to functional redundancy (i.e., the roles of the added species are already performed by other species) (18–20). Hence, stepwise inclusion of one species after another to experimental communities and observation of the associated functioning (e.g., in terms of biomass production) indicate the effect of each newly included species on the functioning in these particular communities.

Another factor may have an impact on the BEF relationship as well: the environmental context (3). The environmental context is important because contemporary ecosystems are facing multiple environmental changes of increasing intensity. To date, BEF relationships have mainly been investigated under a single environmental scenario leaving the effects of potential environmental changes unexplored. Only a few studies have tested the impact of disturbances (21), pathogens (22), drought (17), resource richness (23), and temperature fluctuations (24) on the BEF relationship. Thus, knowledge on the functioning of ecosystems under different environmental conditions after anticipated change is rare but urgently required (25).

Microbial model systems provide a formidable tool with which to address such theoretical ecological questions (26, 27). They offer various advantages: High numbers of experiments can be carried out in small laboratory microcosms, all external factors can be controlled and easily manipulated, and many generations of the focal organisms can be tested (26, 28–31). In contrast to such model systems, investigating natural microbial ecosystems may pose challenges, such as the difficulties in defining and estimating the vast number of bacterial species (32, 33). However, these limitations do not apply to laboratory systems with defined artificial communities containing well-characterized species.

In this study, we used microbial model systems to investigate how species richness, species identities, and potential species interactions affect ecosystem functioning under a different set of environmental conditions. We systematically assembled more than 800 artificial communities, with each containing between one and 12 bacterial species. As an indicator of ecosystem functioning, we

Significance

It is currently unclear how biodiversity loss affects ecosystem functioning. The concept of functional redundancy implies that species loss is compensated by other species contributing similarly to functioning. Functional redundancy can be revealed by the relationship between biodiversity and ecosystem functioning (e.g., biomass growth). The functioning of an ecosystem remains unaffected if redundant species are removed but decreases if the removed species have unique roles. Most research on biodiversity–ecosystem functioning (BEF) relationships hitherto was restricted to one single set of environmental conditions. Using a microbial model system, we explored this relationship in different environments. We found that the environmental conditions are pivotal when drawing conclusions about functional redundancy because BEF relationships drastically differ due to changing species roles and interactions.

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observed the communities' biomass production in three different abiotic environments of increasing abiotic stresses: low benzoate concentration (1 g/L, "environment 1"), high benzoate concentration (6 g/L, "environment 2"), and high benzoate concentration (6 g/L) with NaCl (15 g/L, "environment 3"). Each environmental led to a differently shaped BEF relationship, and thus different levels of functional redundancy as well. Further, for analyzing the effects of particular compositions of species, we developed the concept of "minimal communities." This concept allowed us to go beyond the BEF relationship curves and identify the roles of particular species and potential species interactions for ecosystem functioning.

Results and Discussion

Effect of Species Richness. We found positive BEF relationships under all environmental scenarios. However, the functional form of these relationships (Box 1) was highly sensitive to the environmental conditions (compare black curves in Fig. 1). Its shape shifted from a saturation curve in environment 1 to a nearly linear curve in environment 2, to a rather sigmoidal curve in environment 3 [the separation between growing (blue) and nongrowing (red) communities under each environmental scenario is discussed in *Materials and Methods, Data Analyses*].

In environment 1, biomass production saturated at low species richness (relative species richness $S \approx 0.3$; Fig. 1A) suggesting high functional redundancy. The early occupation of functional niches reduces the contributions of additional species (18, 19). In environment 2, mean biomass production increased almost linearly with species richness (in the considered range of 12 species) and no saturation occurred (Fig. 1B). This observation suggests that any species addition increases ecosystem functioning. However, this interpretation has to be taken with care because biomass growth under these conditions displayed particularly high variances: For all species richness levels, communities tended to separate toward either high or approximately no functioning, pointing to the importance of species identities (discussed below). In environment 3, mean biomass production showed an almost sigmoidal increase with species richness (Fig. 1C). Under these conditions, no species grew as a monoculture. Even for benzoate-tolerant degraders, at least one other species (benzoate degrader or not) was essential for growth and at least five species were needed to achieve growth of more than 50% of the experimental communities.

Box 1: Phenomenological BEF Model

The modified Michaelis–Menten model for BEF developed by Naeem (18):

$$\Delta OD = \frac{F_{max} \cdot S^c}{S_{min} + S^c}$$

was fitted to the communities' biomass production using nonlinear regression [trust-region-reflective least squares algorithm in MATLAB (MathWorks)]. The ΔOD is the change in optical density as a metric of biomass production, estimated as the difference of OD between the start (0 h) and the end (72 h) of the experiment. S is the relative species richness as a metric of diversity, varying between 0 (no species) and 1 (12 species). F_{max} represents the maximum biomass that could be built up under the given environmental conditions ("saturation biomass"). For fitting, we constrained the parameter F_{max} to the highest ΔOD observed for any community in the respective environmental scenario. The coefficient of interaction represents additive ($c = 1$) or multiplicative ($c > 1$) effects of increasing species richness. High values of c indicate strong interaction between species. S_{min} is the minimum species richness for producing a "fair amount" of biomass. Small values express a high species equivalency ("functional redundancy"), and vice versa. For $c = 1$, S_{min} is the species richness required for producing half of F_{max} .

In comparison to environment 1, more biomass was built up by the communities in environment 2 and environment 3 [change in optical density as a metric of biomass production (ΔOD) at relative species richness $S = 1$ (i.e., 12 species): ≈ 0.33 at 1 g/L vs. ≈ 0.76 at 6 g/L and ≈ 0.41 at 6 g/L + NaCl, respectively] due to the sixfold higher substrate concentration. However, although access to minerals and space was provided, both environmental scenarios, on average, did not result in sixfold higher biomass, as might be suspected.

Our experimental results suggested fitting nonlinear BEF relationships that offer additional information (e.g., on functional redundancy) compared with studies considering the slopes of

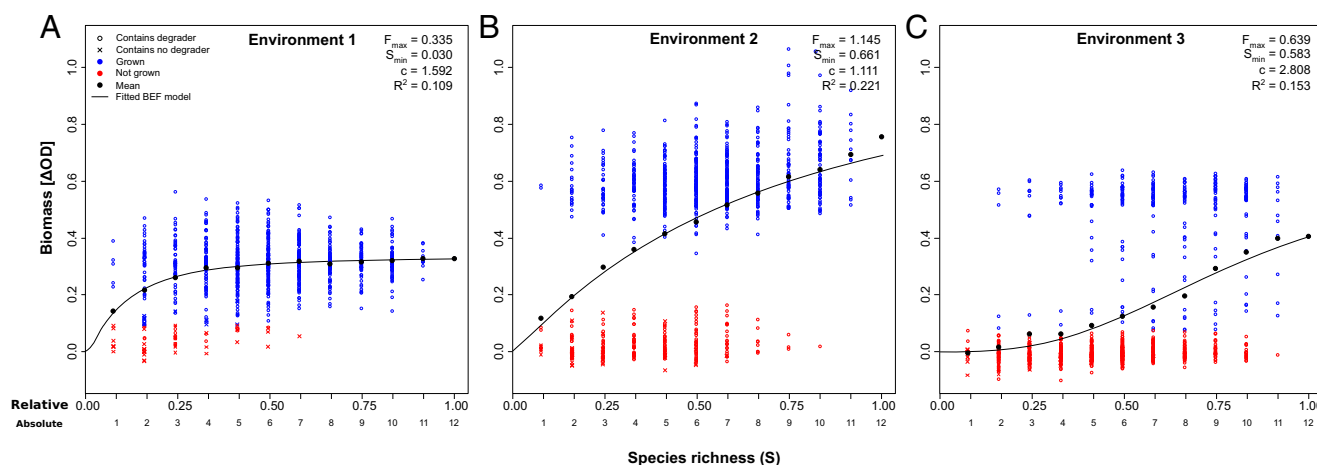


Fig. 1. Biomass production (ΔOD) plotted against species richness in three different environmental scenarios: environment 1, 1 g/L benzoate (A); environment 2, 6 g/L benzoate (B); and environment 3, 6 g/L benzoate and 15 g/L NaCl (C). Communities are differentiated according to those communities containing no degrader (crosses) or at least one degrader (circles). Blue and red symbols indicate growing and nongrowing communities, respectively. For each species richness level, mean values (●) and modeled biomass production were calculated (Box 1). Model parameters include the theoretical maximum biomass (F_{max}), functional redundancy (S_{min}), and coefficient of species interaction (c). Although the fitted BEF model is in good correspondence to the observations' mean values, the R^2 values underpin that functioning strongly depends on species composition in addition to species richness.

Fig. 3. Distributions of species effects on biomass production for each of the 12 species (A–L) in environment 1 (A), environment 2 (B), and environment 3 (C). Species effects were calculated as the difference between biomass production in a community containing a species and biomass production of the corresponding community without that species (compare *Materials and Methods*, *Data Analyses*). Boxes widths span between the 25th and 75th percentiles [i.e., the interquartile range (IQR)], and whiskers extend to 1.5-fold times the IQR. Outliers beyond the whiskers are not plotted.

species growing as monocultures to communities of 12 species, where only the addition of the last remaining species from the given pool enabled biomass growth (Fig. 1C, red circle for species richness 11 but blue circle for species richness 12). Based on the minimal communities, potential specific partners for interactions were identified (*Materials and Methods, Data Analyses*).

As expected, in environment 1, all benzoate degraders (species D, E, F, G, and K) could grow as monocultures (Fig. 44). Under these environmental conditions, species E, F, G, and especially species K were the most frequent activators of biomass growth. Other species, including all nondegraders, could induce biomass growth in the presence of partner species (solid circles in Fig. 44). To a certain degree, these partner species were redundant for the interactions because almost no specific interactions between particular species could be identified from the minimal communities (only one arrow in Fig. 44).

Environment 2 gave a completely different picture (Fig. 4B). The mere presence of either one or both of the two benzoate degraders F and G was always sufficient for biomass growth, and the absence of these two species led to functional breakdown. Interactions or even specific partners for biomass growth could

not be identified (dashed circles for all other species and no arrows in Fig. 4B). This finding is in line with the low coefficient of interaction (parameter c) derived from Fig. 1B and, together with the increase in functioning with species richness, suggests selection effects. Whether species F or G dominated when they co-occurred could not be estimated with the experimental design.

Under the harshest abiotic conditions (environment 3), species interactions were pronounced and no species grew as a monoculture (Fig. 4C). All benzoate degraders needed at least one partner to grow, and all species (also nondegraders) could take over the role of an activator species in particular communities (solid circles in Fig. 4C). As a result, a complex pattern of potential specific interactions between species developed (arrows in Fig. 4C) pointing to complementarity effects in this environment. Here, species F was almost always present in the minimal communities, and thus appears to have a unique role as a partner for interactions under these abiotic conditions (arrows in Fig. 4C).

Methodological Limitations and Transferability to Other Ecosystems.

As in comparable studies, our findings describe relationships between ecosystem functioning and species richness and composition

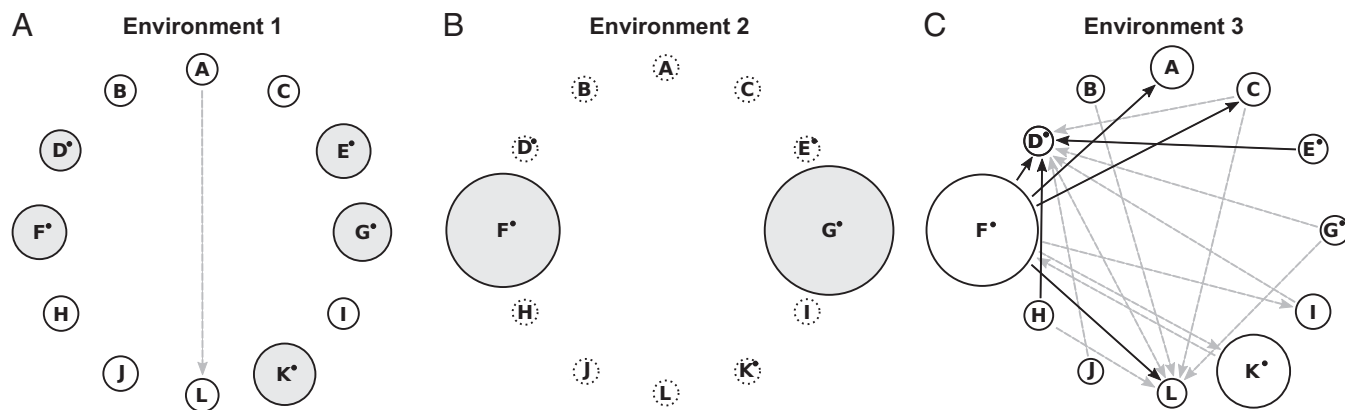


Fig. 4. Species (A–L) interactions estimated from minimal communities ensuring biomass growth (details are provided in *Materials and Methods*, *Data Analyses* and Fig. 2) in environment 1 (A), environment 2 (B), and environment 3 (C). Benzoate degraders are marked with a small filled black circle. Filled gray circles indicate a species' ability to grow under the given environmental conditions as a monoculture. Dashed circles indicate that a species never was the activator species. Otherwise, sizes of solid circles indicate how often a species was the activator species (relative number of all cases in the given environment). Arrows point from a potential partner species to an activator species if the respective partner species was present in either 100% (solid black arrows) or at least 80% (dashed gray arrows) of the corresponding minimal communities. This method reveals potential specific partners for species interactions, which differed strongly among the different environments.

of initially even communities (24). We assume that evenness changed during the experiments in many cases as an outcome of community dynamics under the different environmental conditions, resembling the situation in natural ecosystems. Because we could not measure the changes in each species' relative abundance within the multi-species communities, we did not analytically separate selection and complementarity effects (9, 38). Nonetheless, we could interpret the BEF relationships (Fig. 1) and the discovered species interactions (Fig. 4) concerning the relevance of these effects.

In this study, we explicitly measured biomass production as a general proxy for ecosystem functioning. This proxy represents a robust measure of benzoate conversion into microbial biomass, be it direct or involving trophic interaction between species. An alternative could have been to measure benzoate degradation as a specific process of interest, but doing so would have blurred functioning of the microbial community because it might have included nonproductive transformation of the mother compound into dead-end metabolites, as well as complete mineralization and conversion into biomass. Given the observed considerable differences in species interactions and redundancy in the different environments, it is plausible to assume that the environmental context is similarly important for benzoate transformation as for biomass production from benzoate. The particular shapes of BEF relationships and the potential species interactions obtained from our analysis are specific for the microbial model system considered and the selected proxy for ecosystem functioning.

We cannot rigorously extrapolate this study to natural ecosystems containing other (and potentially many more) species from different domains of life. Our findings, however, that the environmental context may strongly determine the basic shape (nonlinearity) of BEF relationships and the extent of species interactions, and thus the assessment of functional redundancy, provide valuable hypotheses to be tested further with other species types and in different environments. They may also be interpreted as a general hint that species roles for ecosystem functioning can shift substantially after environmental change.

Another aspect of our system is the limited potential to mirror the highly complex structural and temporal context of natural communities. The design and establishment of long-term microbial model systems under natural environmental conditions (39) would be a future challenge. Integrating such systems with information on the microbial genomes, one could even assemble communities in such a way that specific traits and interactions may be more precisely monitored and interpreted.

The three selected environmental scenarios do not allow disentangling whether the decrease in functional redundancy and the importance of species interactions in environment 3 result from the presence of NaCl alone or from the combination of NaCl with a high benzoate concentration. However, making this distinction was not the focus of this study, and it does not affect our general findings that refer to different exemplary environments. These exemplary environments represent different abiotic conditions that can be seen as a result of environmental change. In our setup, we did not manipulate concentrations of benzoate or NaCl in the course of the single experiments. Observing transient dynamics under gradually changing environmental conditions is a potential next step to investigate the impact of environmental change on BEF relationships further.

Conclusions

Our results show that, under altered environmental conditions, high biodiversity can be beneficial to provide not only (*i*) a (set of) species with the relevant traits to thrive in the harsh environment but also (*ii*) potential partners that will allow these species to thrive. However, global environmental change also impairs biodiversity, and therefore may have severe consequences for ecosystem functioning. In particular, our finding that changes in interspecific interactions are essential for ecosystem functioning in different environments is an important step toward a more mechanistic explanation of biodiversity effects under different

environmental conditions and suggests a careful interpretation of functional redundancy.

We found that the shape of the BEF relationship strongly depends on environmental conditions. Thus, initial conclusions concerning species' functional redundancy in a given environmental setting and predictions on the loss of ecosystem functioning due to extinctions of species can be completely misleading when based on a BEF relationship for a given environment alone. Species loss can have an even stronger impact than anticipated when, additionally, the environmental conditions change. As shown here, such changes may result in modified interactions between species determining the functioning of an ecosystem and in an altered shape of the BEF relationship. Thus, taking into account the environmental context challenges the generality of functional redundancy and suggests that the potential of species-rich ecosystems for dynamically constituting positive interspecific interactions when necessary can be much more important than presently believed.

Vice versa, the extent to which the functioning of an ecosystem is maintained under altered environmental conditions strongly depends on its biodiversity. Diverse communities are more likely to contain species with traits pivotal for functioning in different environments. These species may benefit both selection and complementarity mechanisms, because they can be essential performers (e.g., biomass producers) or essential partner species for positive interspecific interactions. Species dismissed as functionally unimportant under present conditions may be required for future ecosystem functioning under altered conditions.

Our findings have potential consequences for the management of ecosystems in that they highlight the importance of diversity for maintaining ecosystem functioning, especially under altered, more extreme environmental regimes.

Materials and Methods

Experimental Design. We conducted experiments with assemblages randomly drawn from a pool of 12 bacterial species (the species list is provided in Table S1). The species for the pool were selected such that they cover equal environmental requirements and growth performances, allowing for coexistence but also differences in certain specific metabolic characteristics. The pool included five species capable of directly using benzoate (which served as the sole carbon source; compare below), whereas seven species were incapable of directly using the resource provided. It cannot be clearly inferred from our experiments whether the latter species might potentially grow on intermediate metabolites of benzoate degraders. However, including these species enhances the potential for complementarity effects (24). We assembled 883 random communities (about 20% of all 4,095 theoretical assemblages possible) across all richness levels (ranging from single species monocultures to the 12-species combination) in multiwell plates. The number of random assemblages per richness level was chosen according to the respective maximum number (Fig. S1). The specific combination of species traits yielded random communities potentially covering a range from high functional redundancy to high, albeit undefined, functional differences. In each random community, total cell abundance was adjusted to be equal at the start of the experiment but most likely diverged during the incubation period. To avoid space limitations during growth, the chosen well volume was much larger than the volume required for the maximum possible build-up of biomass with the given amount of benzoate.

To assess how identical communities behave in different environments, we used benzoate as the sole carbon source and systematically created the following external abiotic conditions to be applied to the whole set of random assemblages: (*i*) benzoate at a low concentration (1 g/L), causing high competition among degrading species for the limited resource (environment 1); (*ii*) benzoate at a high concentration (6 g/L), reducing resource competition due to the copious resource but simultaneously exerting toxic stress from the high benzoate concentration on some species (environment 2); and (*iii*) the same high benzoate concentration (6 g/L) with NaCl (15 g/L) exerting additional osmotic stress (environment 3).

Laboratory Setup. All 12 bacterial strains (the taxonomic names are provided in Table S1) were freshly prepared from -80°C glycerol stocks. Fresh cultures were prepared by incubation for 24 h at 30°C in CASO (casein-peptone-soymeal-peptone)-mineral salt medium (Merck) (a detailed overview of the procedure is illustrated in Fig. S2). The final working suspensions were created by adjusting washed cells to 2×10^9 cells per milliliter of fresh medium by flow cytometry. Microcosms with random communities across all species richness

levels were assembled from the working suspensions by a pipetting robot (BioMek 2000; Beckman Coulter) into microwell plates (96 wells with a 0.5-mL volume each) containing mineral salt medium, supplemented by the respective amounts of benzoate and NaCl for generating the different environments as described (compare *Experimental Design*). The communities' initial total cell concentrations were 2×10^6 cells per milliliter for all wells and species combinations. Exactly the same experimental communities were established for each environmental scenario.

Community biomass production (Fig. 1) was estimated through OD as a proxy for ecosystem functioning, indicating how well a community containing specific species with certain individual traits performs under a given environment. OD was determined spectroscopically measuring light absorbance at a wavelength of 590 nm with an automatic plate reader (BioTek) and used to calculate the ΔOD , the difference between initial OD and OD after 72 h of incubation for each experimental community. After 72 h, all communities had reached a stationary phase with no further change in biomass.

Data Analyses. Differentiation between nongrowing (red in Fig. 1) and growing (blue in Fig. 1) communities was achieved separately for each environmental scenario, using a statistical two-component probability mixture model approach (with $\alpha < 0.05$ for separation) (40, 41). Parameter values for the phenomenological BEF model (Box 1) were fitted using the trust-region reflective least squares algorithm in MATLAB, version 2013a (MathWorks), constraining F_{max} to the maximum observed ΔOD in each environment.

For investigating a species' (positive or negative) effect on biomass production (ΔOD_{Diff}) in a given experimental community, we calculated the difference in ΔOD values of the community with and the community without that particular species (compare Fig. 2). The species' overall effects on biomass production (Fig. 3) were then assessed by collecting the species' ΔOD_{Diff} values from all communities for which the corresponding community without that

species existed in our set of investigated species assemblages (compare *Materials and Methods*, *Experimental Design* and Fig. S1). The estimation of positive, negative, or neutral overall effects (median above, below, or equal to zero) was based on the Wilcoxon test (with $\alpha < 0.05$) and calculated with R, version 3.1.2 (40).

To elucidate species interactions, the concept of activator species and minimal communities was developed (a detailed explanation is provided in the legend for Fig. 2). In the minimal communities, we analyzed which other species (potential partners) were present in the previously nongrowing communities that resulted in growth after inclusion of a relevant activator species. To obtain specific partners for interactions on a reasonable basis, we only included cases where a species was the "activator" in at least five different minimal communities. For each of these activator species, other species occurring in 100% (strong indication for interaction; solid black arrows in Fig. 4) or in at least 80% (weaker indication for interaction; dashed gray arrows in Fig. 4) of the corresponding minimal communities were classified as potential specific partners. If no species occurred that often, then, obviously, several species could serve as partners for interactions with the activator species (Fig. 4A) or the activator species did not rely on interactions at all (species able to grow as monocultures in Fig. 4 A and B) in the given environment. Corresponding calculations were performed in MATLAB.

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