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Seed size is heterogeneously distributed among destination habitats in animal dispersed plants

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Abstract

Seed size is a central trait in plants, conditioning the probabilities of seed dispersal, predation, germination and seedling survival even within a single species. In wind-dispersed species, seed size is not homogeneously distributed in the seed shadow, and it is clear that this trait influences dispersal distances. However, in animal-dispersed species, it is poorly known how and why the process of seed dispersal determines, per se, the spatial distribution of seed size. We predict that frugivores may generate heterogeneous distributions of seed size on seed rain due to two mechanisms. First, frugivores differing in body size and post-feeding habitat selection may feed on a different array of seed sizes and deposit them in different destination habitats. Second, even feeding on a similar gradient of fruit sizes, frugivores may spend in different post-foraging times at different microhabitats, the more visited microhabitats receiving a larger proportion of small sized, longer-retained seeds. We analyzed the distribution of seed weights at destination microhabitats for three fleshy-fruited tree species, *Taxus baccata*, *Ilex aquifolium* and *Crataegus monogyna*, dispersed by a common guild of avian frugivores in a temperate secondary forest of N Spain. Mean seed weight varied among microhabitats for the two former species, with smaller average weight under the canopy of *Taxus* male trees. We discuss several alternative hypotheses and conclude the spatial segregation of seed weight to be a consequence of frugivore activity, probably related to size-related differences in seed retention time and longer visitation or permanency time in protective microhabitats.

Zusammenfassung

Die Samengröße ist eine zentrale Eigenschaft von Pflanzen, welche die Wahrscheinlichkeit der Samenverbreitung, des Samenfraßes, der Keimung und des Keimlingsüberlebens sogar innerhalb einer einzigen Art bestimmt. Bei Arten mit Windverbreitung ist die Samengröße nicht homogen über den Samenschatten verteilt, und es ist klar, dass diese Eigenschaft die Ausbreitungsdistanzen bestimmt. Bei Arten, die durch Tiere verbreitet werden, ist bisher kaum bekannt, wie und warum der Prozess der Samenverbreitung per se die räumliche Verbreitung der Samengröße bestimmt. Wir sagten voraus, dass Frugivore heterogene Verteilungen der Samengröße über einen Samenschatten aufgrund von zwei Mechanismen generieren. Erstens könnten Frugivore unterschiedlicher Körpergröße und mit unterschiedlicher Habitatwahl nach dem Fressen unterschiedliche Bereiche in der Samengröße fressen und sie in verschiedenen Zielhabitaten absetzen. Zweitens könnten Frugivore, auch wenn sie einen ähnlichen Bereich der Fruchtgröße nutzen, nach dem Fressen unterschiedliche Zeiten in unterschiedlichen Mikrohabitaten

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verbringen, wobei die häufiger besuchten Mikrohabitate eine größere Portion der kleineren, länger zurückgehaltenen Samen erhalten. Wir analysierten die Verteilung der Samengewichte in Zielhabitaten bei drei Baumarten mit fleischigen Früchten: *Taxus baccata*, *Ilex aquifolium* und *Crataegus monogyna*, die durch eine weitverbreitete Gilde von frugivoren Vögeln in gemäßigten Sekundärwäldern Nordspaniens verbreitet werden. Das mittlere Samengewicht variierte bei den zwei zuerst genannten Arten zwischen den Mikrohabitaten, mit einem geringeren Durchschnittsgewicht unter dem Dach von männlichen Taxusbäumen. Wir diskutieren einige alternative Hypothesen und schließen darauf, dass eine räumliche Trennung aufgrund des Samengewichtes eine Konsequenz der Aktivität der Frugivoren ist und möglicherweise in Verbindung zu den größenabhängigen Unterschieden in der Samenzurückhaltung und den längeren Besuchs- oder Verbleibzeiten in geschützten Mikrohabitaten steht.

Keywords: Seed dispersal; Seed weight; Microhabitat; Spatial heterogeneity

Introduction

Most studies on seed dispersal consider as a premise the recruitment advantage derived from seeds being deposited far from the parent plant. This advantage is supposed to derive from the escape from high propagule aggregation near the mother plant, which promotes disproportionate mortality by density-dependent pathogens and predators, kin competition and competition with the mother plant (Janzen 1970; Loiselle 1990; Terborgh, Pitman, Silman, Schichter, & Núñez 2002). Nevertheless, recent research pointed out that seed aggregation may be also observed far from the parent plants due to the movement pattern of the dispersal vector and to habitat topography (Schupp, Milleron, & Russo 2002). For fleshy-fruited plants, frugivorous animals consume fleshy fruits and disperse the seeds generating a seed shadow that largely reflects their post-feeding habitat use. These dispersers determine the quantity, distance and direction seeds are dispersed and thus the quality of that dispersal (Schupp 1993; Wang & Smith 2002; Levine & Murrell 2003).

The delivery of seeds in different sites with different prospects for seed and seedling survival has important consequences for plant demography. Several studies have considered the quality of the destination microhabitat, the importance of seed density (both homospecific and heterospecific seed clumps) and the ecological context on plant demography during the recruitment period (Rey & Alcántara 2000; Russo & Augspurger 2004; García, Obeso, & Martínez 2005a). However, despite their importance, few attempts have been made to analyse the processes determining the spatial segregation of disseminated seeds in relation to seed size, as well as the post-dispersal consequences of the patterns of seed size distribution.

Seed size affects the probability of predation, germination, seedling survival and establishment in the bird-dispersed tree *Prunus virginiana* (Parciak 2002a, 2002b). In general, larger seeds conferred benefits to seedlings against nutrient limitation, drought, shading, herbivory and competition (e.g. Bond, Honig, & Maze 1999; Jakobsson & Eriksson 2000; Seiwa 2000; Seiwa, Watanabe, Saitoh, Kanno, & Akasaka 2002; Gómez 2004). However, the relationship between seed size and fitness is much more complex than expected from directional phenotypic selection on seed size. In fact, offspring fitness is a product of several components such as dispersal to safe sites, depredation risk, and seedling establishment. Seed size may affect each of these processes in different ways leading to conflicting selective pressures (Alcántara & Rey 2003; Gómez 2004; Martínez, García, & Obeso 2007).

In wind-dispersed plants it has been assumed that there is an inverse relationship between seed mass and dispersal distance (Greene & Johnson 1993), which entails that seed mass variability observed within plant is not homogeneously distributed within the seed shadow. Surprisingly, in animal-dispersed plant species, the effect of seed size on the dispersal process has been rarely considered in connection with the quality of the destination microhabitat. In fact, most studies on the spatial patterns of seed dispersal in zoochorous plants implicitly assume that variability in seed weight is homogeneously distributed in the seed rain (but see Alcántara, Rey, Valera, & Sánchez-Lafuente 2000). Nonetheless, a spatially segregated distribution of seed size may be predicted at the dispersal stage of animal-dispersed species when accounting for several non-exclusive mechanisms. A first mechanism is operating when different disperser species transport a given range of seed weights, for example because they select a different array of fruit sizes depending on their consumption preferences or body size (e.g. Jordano 1984; Herrera, Jordano, López-Soria, & Amat 1994; Rey, Gutiérrez, Alcántara, & Valera 1997). Then, these different dispersers exhibited different spatial patterns of post-foraging movement, visiting more frequently some habitat patches instead of others (Thomas, Cloutier, Provencher, & Houle 1988; Clark, Poulsen, Bolker, Connor, & Parker 2005; Spiegel & Nathan 2007). These effects combined should lead to mean seed weight differences among destination habitats or distances from parent plants, or at least to differences in the magnitude of the variance in seed weight among them. For example, in *Olea europaea* var. *sylvestris*, differential use of the habitat by smaller species of avian dispersers led to an overrepresentation of smaller seeds in open habitats (Alcántara et al. 2000).

Second, and even when transporting a similar gradient of seed sizes, frugivores may generate a spatially heterogeneous seed size distribution when they spend different post-foraging times in different microhabitats and, at the same time, seeds of different size have different gut retention times. In this sense,

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Hedge, Shaanker, and Ganeshaiah (1991) demonstrated in the bird-dispersed tree *Santalum album* that small seeds predominantly passed through the intestine whereas larger seeds were generally regurgitated. Thus, we may predict small seeds to be more represented in those habitat patches where frugivores spend longer time after foraging for fruits at source plants. It is known that some frugivores spend more time in patches or microhabitats that provide spatially aggregated fruit resources or protection against predators when resting (e.g. roosting sites, Russo & Augspurger 2004).

To examine the spatial segregation of seed size variability at the dispersal stage, we analyzed the distribution of seed weights in different microhabitats for three fleshy-fruited tree species: hawthorn (*Crataegus monogyna*), holly (*Ilex aquifolium*) and yew (*Taxus baccata*) in a temperate secondary forest. This system is particularly adequate for such a goal because in previous studies we have shown that these plant species receive a homogeneous spectrum of avian dispersers, which vary in their post-feeding habitat selection (Martínez, García, & Obeso 2008). Results presented here confirm that for a given plant species mean seed weight may differ at the destination microhabitats.

Materials and methods

Study site and plant species

This study was conducted during 2004–2005 at Teixeu, located in Peña Mayor Range (Asturias province, NW Spain). This site included secondary forest stands composed of the focal study species hawthorn (*C monogyna*), holly (*I aquifolium*) and yew (*T baccata*) together with hazel (*Corylus avellana*), and mature deciduous forest stands of beech (*Fagus sylvatica*). Different stand types are intermixed and embedded into a matrix of pasture valleys and rocky slopes.

We studied the seed deposition patterns of three fleshy fruited tree species: *C monogyna* (Rosaceae; henceforth: *Crataegus*), a deciduous shrub or small tree whose fruits are single-seeded drupes red when ripen; *I aquifolium* (Aquifoliaceae; henceforth: *Ilex*), a dioecious evergreen tree that produced red berries containing 2–4 pyrenes (Obeso 1998); and *T baccata* (Taxaceae; henceforth: *Taxus*), a dioecious evergreen tree with arilated seeds that we will denote as "fruits" for simplicity. In the Cantabrian range (north-western Spain), fruit ripening occurs in early September, November and August in *Crataegus*, *Ilex* and *Taxus* respectively.

Fruits are mainly consumed by thrushes:blackbird *Turdus merula*; fieldfare *T. pilaris*; mistle thrush *T. viscivorus*; redwing *T. iliacus*; and song thrush *T. philomelos* (Martínez et al. 2008). Some fruits that fall beneath the canopy of the parent tree are eventually dispersed by carnivorous mammals, such as fox *Vulpes vulpes* and badger *Meles meles*. The fruits of the most specialized species, *I aquifolium*, are mainly consumed by *T. iliacus*. Two other species, *T. philomelos* and *T. viscivorus*, are responsible for the dispersal of *T baccata*. *C monogyna* is the most generalist species, receiving dispersal services by five *Turdus* species, none of them being more important than the others (Martínez et al. 2008).

Fruit size is a surrogate of seed size and the birds select larger fruits early in the fruiting season at least in the case of *Ilex* (Obeso & Fernández-Calvo 2002) and *Crataegus* (Martínez et al. 2007). However at the end of the fruiting season the birds consume the entire crops of *Ilex* and *Taxus*, then nearly all the seeds are dispersed regardless of their size.

To obtain information about seed mass within the population and the distribution of variance of seed mass among and within trees, we collected fruits of *Ilex*, *Taxus* (15 trees per species and 25 fruits per tree) and *Crataegus* (33 trees and 30 fruits per tree, Martínez et al. 2007). The fruits were oven dried and dissected to determine seed dry mass to the nearest 0.1 mg.

Evaluation of seed dispersal

Seed rain was evaluated in five destination microhabitats defined by tree species and tree sex in dioecious species: (1) "Ilex female", (2) "Ilex male", (3) "Taxus female", (4) "Taxus male", (5) "Crataegus". In September 2004, we established fixed 0.5 m × 0.5 m quadrats in the area ($N = 14$ quadrats per microhabitat). For each microhabitat, the quadrats were located beneath 14 individual trees ≥10 cm DBH; ≥5 m apart from other trees, and with none or very low canopy overlap among conspecific trees. The initial design also included "open habitat" (dominated by pasture and rocks), "beneath *F. sylvatica*", and "beneath *C. avellana*" (see Martínez et al. 2008 for details), but due to the reduced number of seeds that were sampled in these microhabitats they were excluded from the comparisons among habitats to avoid highly unbalanced ANOVAs. Although the cover of these habitats represents 55% of the study area (García, Obeso, & Martínez 2005b), they only received 9.5% of the dispersed seeds for all species combined.

Taking into account that the distance to the possible source of seed rain (e.g. nearest conspecific producing fruits) determines the number of seeds arriving at the sampling quadrats (see Martínez & González-Taboada 2009 for dispersal kernels within the same locality), we measured the distance to the nearest *Ilex* female, *Taxus* female and *Crataegus* tree trunks for each sampling quadrat, even in the case the fruiting tree was the same as the species of interest.

From September to January, we collected all dispersed seeds from the quadrats once per month. All quadrats were sampled for all three species of seeds. Two quadrats beneath *Ilex* males did not receive *Taxu*s seeds and five quadrats (three beneath *Ilex* males, one beneath *Taxus* male and one beneath *Taxus* female) did not receive *Crataegus* seeds. Samples were oven dried at 60 °C for 24 h, and all seeds were identified to the species level, counted and individually weighed to the nearest 0.1 mg. We obtained a mean seed weight per quadrat for each of the three species.

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Q1 **Table 1.** ANCOVAs examining the effect of the distance to the nearest conspecific fruiting tree and microhabitat type on the seed mass at destination (log-transformed data).

Source of variation	d.f.	MS	*F*	*P*
Taxus baccata				
Distance to conspecific	1	0.00029	0.110	0.745
Microhabitat	4	0.03037	2.770	**0.035**
Error	62	0.17002		
Ilex aquifolium				
Distance to conspecific	1	0.00009	0.030	0.872
Microhabitat	4	0.01278	3.910	**0.007**
Error	64	0.00327		
Crataegus monogyna				
Distance to conspecific	1	0.00074	0.085	0.772
Microhabitat	4	0.01441	1.659	0.172
Error	57	0.00868		

Differences among microhabitats in the weight of deposited seeds were tested by ANCOVAs using the distance from the sampling quadrat to the nearest conspecific producing fruits (distance to the nearest *Ilex* female, *Taxus* female and *Crataegus* for *Ilex*, *Taxus* and *Crataegus* seeds respectively) as a continuous predictor. We considered that the possible underestimation of seed rain due to undetected seed removal from sampled surfaces was negligible because, first, seed removal by diurnal animals was never observed. Second, seed removal by nocturnal rodents is low during most of the dispersal season: predation frequency peaks in winter, long after the peak of dispersal season.

Results

Mean seed mass (±SD) for samples collected from trees was 64.6 ± 8.5 mg ($N = 375$) for *Taxus*, 31.3 ± 9.1 mg ($N = 375$) for *Ilex*, and 68.8 ± 15.0 mg ($N = 978$, Martínez et al. 2007) for *Crataegus*. Percentage of variance in seed mass accounted for by within tree level was 50% for *Taxus*, 61% for *Ilex* and 46.5% for *Crataegus*. Average mass of dispersed seeds, including all destination microhabitats, was 62.9 ± 10.9 mg ($N = 887$) for *Taxus*, 30.3 ± 9.2 mg ($N = 2124$) for *Ilex*, and 71.5 ± 18.4 mg ($N = 513$) for *Crataegus*. The coefficients of variation were 25.7%, 30.4% and 15.8% for *Crataegus*, *Ilex* and *Taxus* respectively. Mean seed weight differed among microhabitats for *Taxus* and *Ilex* (Table 1). Lighter *Taxus* seeds were collected beneath male trees of *Taxus*. *Ilex* seeds were heavier beneath *Crataegus* and females of both *Taxus* and *Ilex* trees and were lighter beneath male trees of *Taxus* (Fig. 1). No differences among microhabitats were found in the case of *Crataegus* (Table 1 and Fig. 1).

Mean distance of sampling quadrats to the nearest conspecific source of seeds did not differ among microhabitats ($F_{(3,\,52)} = 0.436$, $P = 0.728$ for *Taxus*, $F_{(3,\,52)} = 0.719$, $P = 0.545$ for Ilex; and $F_{(3,\,52)} = 2.477$, $P = 0.072$ for *Crataegus*) when the corresponding microhabitat was removed from the analyses (e.g. distance from the quadrats beneath *Ilex* females to the nearest *Ilex* female).

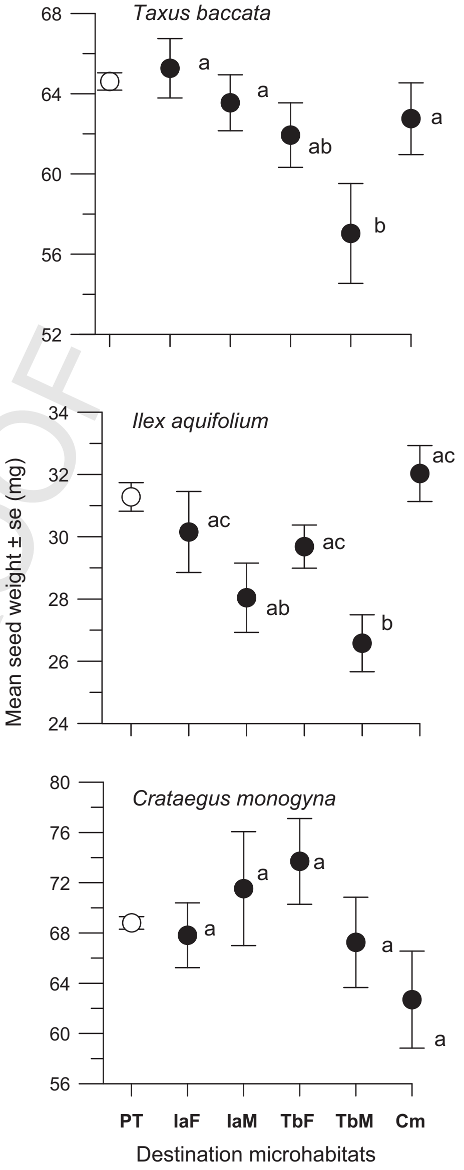

Fig. 1. Mean (±SE) seed weight for different seed species in the destination microhabitats: (PT) "Parent tree", seeds collected on trees (open dots); (IaF) "*Ilex aquifolium* female"; (IaM) "*Ilex aquifolium* male"; (TbF) "*Taxus baccata* female"; (TbM) "*Taxus baccata* male"; (Cm) "*Crataegus monogyna*". Different letters denote significantly different means ($P < 0.05$, LSD test).

Discussion

These results clearly show that at least in some species, the variability in seed weight is not homogeneously distributed among destination microhabitats. Thus, dispersers actually

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generated a heterogeneous distribution of seed weight on the seed rain, even in the case of *Taxus*, that is, the species showing the lowest seed weight variability.

Heavier *Taxus* and *Ilex* seeds were collected beneath fruit producing trees and lighter seeds were disproportionately delivered beneath male *Taxus* trees. This latter microhabitat is a site where birds may spend their resting time away from feeding sites, which might be predation prone places. If frugivorous birds stay for a longer time in this microhabitat they can defecate all the seeds including the lighter ones that should be the last to be defecated. Considering that lighter seeds are passed over a longer period of time (Levey 1986), heavier seeds are expected to be delivered on the first place. Furthermore, heavier seeds generally have a higher probability of being regurgitated (Sorensen 1984; Hedge et al. 1991).

Different avian dispersers might select a different fraction of fruit crops, but this could not be regarded as a satisfactory explanation in this particular case. First, at the study site the seeds of these species are exclusively dispersed by *Turdus* species which do not differ very much in beak and gape size. Thus all *Turdus* species presumably consume the entire range of fruits sizes of the three tree species. Also, *T. iliacus* is responsible for the dispersal of most of *Ilex* seeds (Martínez et al. 2008), which means that differences among microhabitats in the weight of these seeds should be mostly attributed to the activity of only one frugivore species. Finally, the seeds of *Crataegus*, which is the most generalist species, did not differ in mean weight among microhabitats, despite that they were dispersed by the five species of *Turdus*, none of which was particularly more important than the others.

Thus, the causal mechanisms behind the distribution of seed weights can be attributed to bird behaviour and seed retention time. The sequence of bird movements from feeding to post-feeding and resting microhabitats, and budget time at each microhabitat, combined with retention time in relation to seed weight, may determine that different microhabitats receive different fractions of seed weight variability. Then microhabitats not only received different amounts of seeds but also different qualities of delivered seeds.

As an alternative hypothesis we can establish that the heterogeneous distribution of seed weight among different microhabitats might be a consequence of the spatial distribution of the microhabitats relative to source trees providing different seed weights, combined with random bird movements, rather than an effect of the microhabitat itself. Nevertheless, there are four points supporting the effect of the microhabitat.

First, the distance of the sampling quadrats from the possible source of seeds did not differ among microhabitats, which suggests an effect of the microhabitat itself rather than an effect of the distance from source tree to destination microhabitat.

Second, the distance to the nearest conspecific producing fruits had no significant effect on mean seed weight. Then, the differences among microhabitats in mean seed weight were independent of the distance to the possible sources and, consequently, of the spatial distribution of the destination microhabitat.

Third, destination microhabitat might be a consequence of random bird behaviour combined with a patchy distribution of different tree species. However, the analysis of the spatial distribution of the trees in the study area showed that there was not negative association of tree species at small scales, but more than 40% of the trees formed multi-species clumps of two or more trees which had a diameter of four meters (Martínez, Wiegand, González-Taboada & Obeso 2010). In the same way, García, Martínez, and Obeso (2007) analyzing data on distances among heterospecific canopies found that tree species did not show a clumped distribution but were intermingled at the same study site.

Fourth, birds do not move at random, they select the destination microhabitat after leaving the feeding tree. Departures from *Ilex* feeding trees had preferably *Ilex* (54%) and *Taxus* (42%) as destinations (Martínez et al. 2007). Birds feeding on *Taxus* selected *Ilex* as a first perch (42%) followed by *Taxus* (16%) and *Crataegus* (16%) (Martínez et al. 2007).

We have no information about the provenance of the seeds collected in the sampling quadrats, which means that both within- and among-plant variability may be the sources of the gradients of seed weight found here. Considering that an important amount of variance in seed weight was found at the within plant level (Obeso 1998; Martínez et al. 2007, and present results), the patterns of seed mass distribution probably indicate that dispersers deliver a different fraction of individual tree seed crop at different microhabitats. If this is the case, then important consequences for individual plant fitness should be expected.

The pattern of spatial segregation in seed size shown here could also result from differential post-dispersal seed predation by rodents, because they have the potential to select different seed sizes (Martínez et al. 2007). However, there are two lines of arguments against this hypothesis. First, seed predation by rodents examined experimentally peaks in winter after the peak of the seed dispersal season. Additionally, the method of estimation of seed rain by monthly collection of seeds in open quadrats was validated using seed-traps within the same Cantabrian locality (García et al. 2005a, 2005b). Second, even if seed predation had a significant effect on seed size distribution there are not reasons to think that this effect varies among microhabitats. Seed predators are of the same size (*Apodemus sylvaticus*/*flavicollis*) and occur in all microhabitats as demonstrated by the presence of rodent trash heaps at the bottom of trees of the three species (Martínez et al. 2007). Rodent density and antipredator behaviour, which might determine both different levels of seed predation or different seed size selection, is expected to be the same in all microhabitats. One would expect open and covered habitats to differ in predation rate and antipredatory behaviour of rodents but not in the case of microhabitats covered by trees of similar size. Finally, mean weight of seeds from quadrats did not differ from mean

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seed weight of samples collected from trees within the same locality.

In summary, seed weight may differ among destination microhabitats, which means that, as in the case of wind-dispersed plants, seed weight variability is not homogeneously distributed within the seed rain for animal-dispersed plants. The main difference with wind-dispersed plants is the high predictability of this system, in which it is assumed that there is an inverse relationship between seed weight and dispersal distance (Greene & Johnson 1993). In the case of animal-dispersed seeds the distribution of seed weight variability is dependent on the spatial distribution of the microhabitats. Finally, it remains a challenge to determine whether these differences in seed size entail demographic consequences.

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