Farmland biodiversity: is habitat heterogeneity the key?

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Agricultural intensification has led to a widespread decline in farmland biodiversity measured across many different taxa. The changes in agricultural practices affect many different aspects of the farmland habitat, but agricultural industry, policy and much previous research has tended to be concerned with specific sectors or practices (e.g. pesticide use or cereal husbandry). Here, we review the empirical literature to synthesize the research effort that has been directed to investigate specific practices or goals to make general statements regarding the causes and consequences of farmland biodiversity decline. We argue that the loss of ecological heterogeneity at multiple spatial and temporal scales is a universal consequence of multivariate agricultural intensification and, therefore, that future research should develop cross-cutting policy frameworks and management solutions that recreate that heterogeneity as the key to restoring and sustaining biodiversity in temperate agricultural systems.

The second half of the 20th century saw a revolution in agricultural practice, which surpasses any previous agricultural revolution [1]. Economic and technological incentives to increase agricultural productivity in post-war Europe and North America have resulted in unprecedented rapid agricultural intensification over the past 60 years [2,3], which has caused widespread declines in farmland biodiversity in recent decades. Of particular note, and recent concern, has been the decline in populations of birds. In the UK, ten farmland bird species, including the skylark *Alauda arvensis*, tree sparrow *Passer montanus*, linnet *Carduelis cannabina* and starling *Sturnus vulgaris*, have declined by ten million breeding individuals over the past 20 years [3], and there is evidence of widespread declines throughout much of the rest of Europe [4]. Fuller *et al.* [5] found that, between 1970 and 1990, 86% ($n = 28$) of farmland bird species had reduced ranges and 83% ($n = 18$) had declined in abundance. Siriwardena *et al.* [6] confirmed the patterns of changes in abundance: of 13 specialist farmland birds, 11 had declined (seven significantly) and only two had increased (both significantly). Of the 11 declining species, the populations in 1995 were, on average, 52% of the size that they were in 1968 (median = 59%, range = 17–87%). Broadly similar patterns of decline have been shown for other taxa, including mammals [7], arthropods [8] and flowering plants [8].

There is now much evidence to suggest that the decline in farmland biodiversity is related to changing farming practices. On a European scale, the change in cereal yield accounts for 30% of the decline in farmland bird numbers alone [4]. On a regional scale, there are associations between bird numbers and farming practice in England and Wales [9], and associations among farming, insect populations and birds in Scotland [10]. Red-winged blackbird *Agelaius phoeniceus* declines are associated with long-term changes in farming practice in Ohio, USA [11], and butterflies might be declining in northwest Europe because of changes in food-plant abundance across the farmed landscape [12]. On a farm scale, comparison of organic and conventional farms often indicates increased biodiversity in the former in both Europe and North America (e.g. birds [13–15], arthropods [16–18], soil organisms [19,20] and weeds [21,22]), and farms in the UK applying targeted management to encourage wildlife (so-called agri–environment schemes) have elicited increases in the numbers of some bird species [23,24]. On the scale of specific farming practices, links have often been shown between the farming and its ecological impact: no-tillage systems increase soil biomass above that of conventional tillage systems [25], agrochemical use affects vegetation structure and biodiversity, invertebrates and vertebrates [26–28], the husbandry of crops and grassland affects the density and breeding success of birds nesting or feeding in the same fields [13,29–31], and the management of hedgerows and other field margin and boundary vegetation affects the abundance and diversity of flora, invertebrates and birds [32–34] (Fig. 1).

That agricultural intensification has been a main cause of farmland biodiversity losses is now clear. The 1990s was largely a decade during which the problem of biodiversity declines on European farmland was identified and research tended to tackle manageable subsets of the overall problem (e.g. the indirect effects of pesticides on bird populations), with the aim of altering specific aspects of agricultural management to yield benefits for particular species or groups of species. Now the general problem has been identified, we need to look forward to find general solutions rather than specific solutions based on manipulating each individual farming practice. In the 1960s,

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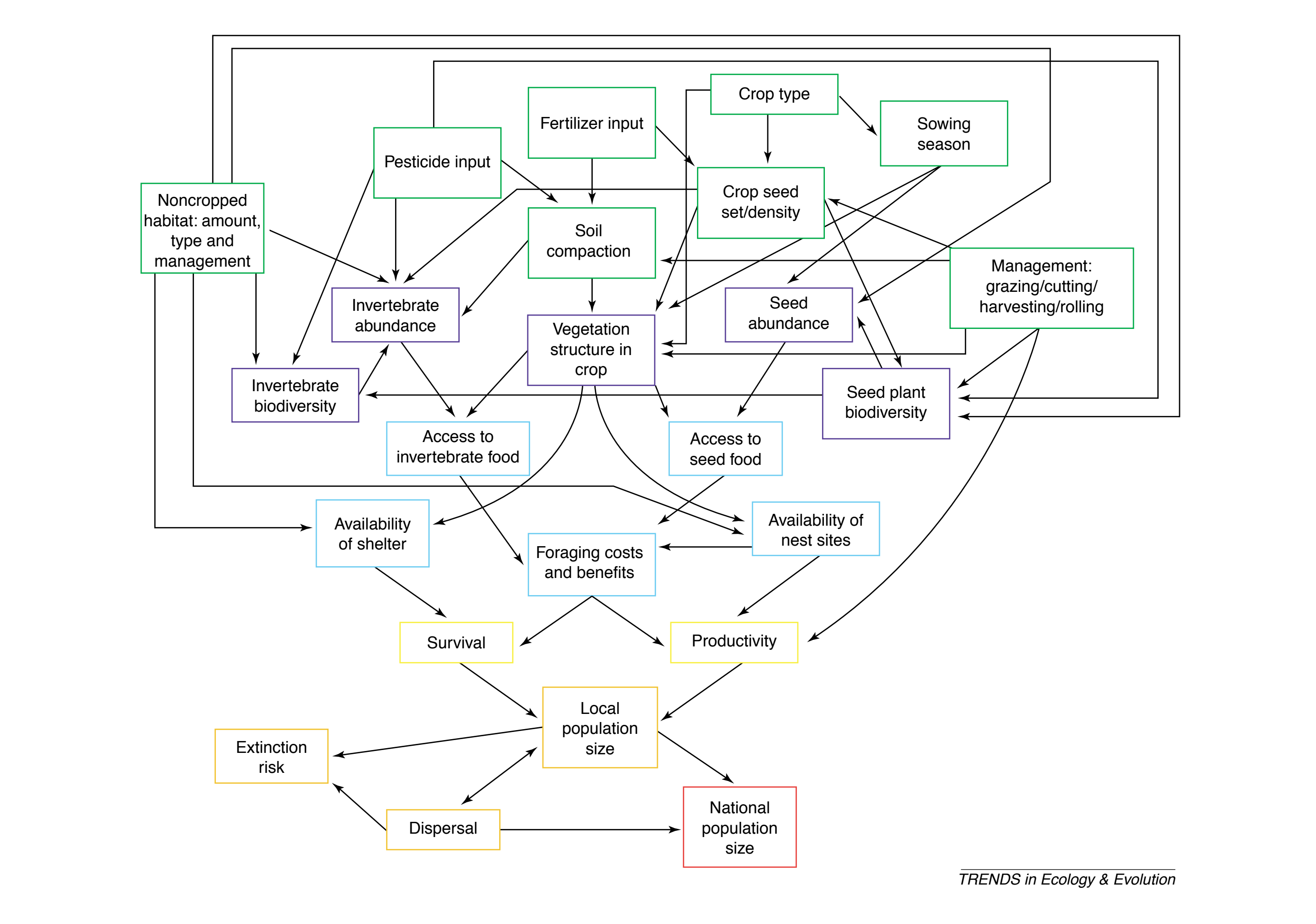

Fig. 1. The multivariate and interacting nature of farming practices and some of the routes by which farming practice impacts on farmland birds. Arrows indicate known routes by which farming practices (green boxes) indirectly (dark-blue boxes) or directly (light-blue boxes) affect farmland bird demography (yellow boxes), and therefore local population dynamics (orange boxes) and finally total population size (red box). The goal of manipulating farming practice is to impact on population size. Rather than identifying key routes through this web to change in a piece-wise fashion (e.g. insecticide usage), we suggest that management designed to increase habitat heterogeneity is likely to benefit the organisms in such a way as to meet the management goals. The rate at which the birds will feed is determined both by the amount of food (abundance) and its accessibility (access) within the habitat.

The Silent Spring [35] drew the world's attention specifically to the indiscriminate toxicity of early generations of agricultural pesticides and, by so doing, suggested the management solution. Here, we review the recent empirical literature and argue that rather than any particular farming practice causing current biodiversity decline, such as pesticide use or changes in noncropped habitat, the multivariate effects of agricultural practices interact very strongly (Fig. 1) and should be considered collectively, rather than individually. We argue that a universal consequence of multivariate agricultural intensification is the replacement of heterogeneity in habitat structure, in time and space, with homogeneity (Table 1, Table 2); habitat heterogeneity is a useful multivariate measure of the intensity of farming. This argument suggests that, rather than concentrating on particular farming practices, there is an identifiable universal management objective – promoting heterogeneity – that could be applied widely across agricultural systems. We focus necessarily on Europe because a large proportion of Europe's biodiversity is found on agricultural land compared with other areas, leading to this being a focus of conservation concern [3]. In a Web of Science search of the terms 'farmland birds' (and related synonyms) for the period Jan–Nov 2002, 70% (40/57) of the papers reported studies from Europe, and only 25% (14/57) from North America.

Heterogeneity matters

Here, we summarize the biological literature to show that habitat heterogeneity is associated with higher biodiversity in the farmed landscape, whether measured at a small or large scale. The evidence that specific agricultural practices reduce heterogeneity is outlined in Table 1 (and summarized in Fig. 1).

The landscape scale: between farms to across regions

Several studies, in Europe and North America, which have mapped the habitat at a scale above that of individual farms, have shown heterogeneity to be associated with diversity. For example, there is a positive relationship between abundance of butterflies in 5-km squares and the heterogeneity [36], and diversity in habitat (measured in 1-km squares) is associated with higher skylark abundance [37,38]. More generally, seed-eating birds, particularly those that are dependent on cereal grain or annual weed seeds, occur in higher numbers in pastoral areas

Table 1. Some of the spatial mechanisms causing increased homogeneity of agricultural habitats in Britain as a result of agricultural intensification

Cause	Consequence for heterogeneity	Refs
Between nations		
Common Agricultural Policy	Starkly differing rates of agricultural intensification between EU and non-EU countries, with rates of biodiversity loss especially high in EU nations with high proportions of land under tillage crops	[4]
Between farms and between regions		
Farm unit specialization (livestock versus arable)	Larger contiguous areas (regions) dominated by either tilled land or grassland, replacing landscapes formerly characterized by mixed farming systems with spatially intimate mixes of tillage and grassland	[65,89]
Consolidation of farm units	Agriculture increasingly dominated by fewer larger farm units and hence larger contiguous areas under common management systems and/or crop rotations	[2,86]
Between fields		
Simplified crop rotations	A reduction in the botanical and structural variety of crops and grassland grown on a single farm, increasing the probability of larger blocks of land being under the same management at any given time	[89]
Removal of noncropped areas	Loss of seminatural habitat features, such as ponds, uncropped field margins and scrub. Recently in the UK, some of these changes have begun to be reversed through positive management of noncropped management features through agri–environment scheme support	[32,88]
Removal of field boundaries	Larger fields, and hence larger contiguous areas under identical management, as a consequence of maximizing efficiency of operation of agricultural machinery and reduce management costs in arable systems where hedgerows and other field boundary structures no longer serve stock-proofing functions	[90]
Within fields		
Mechanization	More uniform swards owing to mechanized, high-precision sowing	[59]
Agrochemical use	Nutrition and protection of crops increases uniformity of establishment and subsequent growth, and reduces species and structural diversity of vegetation by killing and shading out of noncrop species in favour of dense, homogeneous crop swards	[83,84]
Drainage/Irrigation	Soil moisture has important effects on yield, so drainage and irrigation are designed to maximize yield, which results in more uniform establishment and crop growth	
Crop breeding	Increased competitive ability of crop relative to noncrop species encouraging monocultural vegetation cover in combination with agrochemical use	[83,84]
Grassland improvement	Reduction in species diversity by killing weeds, re-seeding with palatable, competitive grass species and favouring those species through drainage and fertilizer use	[60]
Increased duration and intensity of grazing on improved fields	Reduced vegetation height and structural heterogeneity owing to higher grazing intensity and lack of unpalatable species in improved swards	[60,87]

containing small areas of arable land than occur in pure grassland landscapes [39]. For invertebrates, the diversity of generalist insects in crops increases with habitat diversity [40], and habitat diversity enables source populations to repeatedly seed sink populations within intensively managed fields [41,42].

Between-field scale

A mosaic of different fields connected by noncropped habitat, which can provide for a diversity of needs (such as refuges, feeding areas and dispersal corridors), is, *a priori*, expected to aid species persistence and thus biodiversity in general. A field-scale mosaic benefits breeding birds [43], ground beetles [44], spiders [42] and butterflies [36]. In a survey of 72 field sites in Ontario, Canada, Freemark and Kirk [15] show that there is a gradient from sites with many bird species, associated with greater habitat heterogeneity, to sites with fewer bird species, associated with large fields and intensive agriculture. Studies in the UK and Switzerland show that skylark productivity is so low on farmland that pairs must make two or three nesting attempts per year to ensure population stability. The height and density of vegetation within agricultural fields is the main constraint on whether a territory holds habitat suitable for skylark nesting. Where the prevailing farming regime provides a high spatial and seasonal diversity of crop structure in a mosaic of small fields, a higher density of skylarks is able to settle and make multiple nesting attempts than in landscapes with low crop diversities and large field sizes [13,37,45].

A component of between-field heterogeneity in the farmed landscape is supplied by noncropped habitat, such as field margins (e.g. grass margins and strips), linear scrub along field boundaries (e.g. hedges), woodland, ponds, ditches and fallow land. Many studies have highlighted the importance of noncropped habitat in maintaining farmland biodiversity: for weeds [32,33,46], insects [47] (hedges affect beetle numbers even up to 1 km away [41]), spiders [28] and by providing nesting and foraging habitats for birds [48]. The benefits of noncropped habitats for different taxa also interact. For example, plant biodiversity might be greater, attracting herbivorous insects that, in turn, attract their own natural enemies. Field margins might also create an edge effect in fields, either by enhancing food resources (weeds or invertebrates) within the fields and/or enabling birds or mammals to forage close to cover [41,49–51]. As a result, birds and mammals often use field edges far more than they use areas further into the field [33,49,50,52]. How the noncropped habitat is managed is important because

Table 2. Some of the temporal mechanisms causing increased homogeneity of agricultural habitats in Britain as a result of agricultural intensification

Cause	Consequences	Ref
Simplification of crop rotations	Continuous cropping and loss of ley grassland and fallowed land means that fields remain under similar and agriculturally productive management for longer continuous periods	[89]
Mechanization and increasing power of agricultural machinery	Agricultural operations (e.g. sowing and harvesting) can be completed more quickly and are less limited by weather conditions. More fields are therefore in the same state of management at any one time	[85]
Agri–environment schemes	Management prescriptions generally serve to increase heterogeneity, but regulations binding farmers to threshold dates for operations (e.g. weed control on set-aside land) can reduce spread in timing of management operations that would previously have occurred	[86]
Crop breeding advances and agrochemical nutrition and protection of crops	Crops are in the ground for a greater proportion of the year (e.g. autumn sowing of cereals replacing spring sowing) with reduced fallowing and use of break crops or undersowing	[89]
Grassland improvement	Multiple harvesting of forage grasses within a season leads to highly synchronized and rapid harvesting with reduced spatial variation in growth stage of grass crops in different fields	[76]

different species have different habitat requirements. For example, the complexity of a field boundary (whether it is a dense hedge, an open hedge or no hedge at all) will determine which birds use it [34,53–56].

Noncropped habitat also has an important role in providing dispersal corridors and islands in a fragmented landscape to enable movement of individuals across the wider landscape. For example, hedges act as wildlife corridors for birds [34] and beetles [57,41]. Strips of natural vegetation through organically managed Californian vineyards enable the rapid dispersal of natural enemies throughout the crop, and so enable efficient pest control [58].

Within-field scale

The structure of vegetation within the field is increasingly being noted as an important factor in farmland ecology. For example, increasing the density and uniformity of crop planting is an efficient and chemical-free way of suppressing weed growth [59]. Heterogeneity often occurs within fields even though they might appear to be remarkably uniform. Differential seed set or grazing [60], or edaphic factors, can contribute differentially to plant growth, leading to some patches with larger plants, more open structure, or weed presence. This, in turn, contributes to patchiness in insect presence within fields, which then leads to advantages for other animals: for example, spiders are good at finding such insect-rich patches [61], carabid beetles form marked and persistent spatial aggregations within fields [62], and birds can select such arthropod-rich patches when foraging [63].

Birds have varying vegetation structure requirements simply because vegetation structure affects the accessibility and visibility of both potential prey and potential predators [64], and different species have different anti-predator responses. For example, many gamebirds and wildfowl rely on avoiding detection by predators by nesting and foraging in dense vegetation, whereas plovers and skylarks select relatively sparsely vegetated open ground because they depend on early detection of approaching predators [43,65,66]. Similarly, many passerines select relatively sparsely vegetated ground to forage because this provides greater accessibility to food and might enable predators to be detected earlier [30,67–69]. The same birds might, however, use dense vegetation as individual protection once a predator is detected. In some cases, the homogeneity of vegetation cover might, in itself, make birds or their nests more conspicuous to predators. Uniform grass swards, such as those created by intensive grazing with sheep, could increase the likelihood of a predator detecting nests, chicks or adults, because, against a uniform background, camouflage might be decreased [70].

The distribution of vegetation patches that are suitable for nesting and foraging is also crucial. Altricial birds are typically central-place foragers in the nesting season, and need to travel to food-rich patches to forage before returning to the nest. The costs of traveling between multiple patches can become unsustainable if the habitat becomes too fragmented [71], but, to some extent, parent birds are able to absorb the cost of searching for food-rich patches in a food-poor environment. By contrast, in precocial birds the young will bear any costs associated with reduction in the availability of food-rich patches. Consequently, it is perhaps no coincidence that the grey partridge *Perdix perdix* remains the farmland bird species in the UK for which there is strongest evidence that reduction in breeding-season food supplies is a key cause of decline. In altricial species, parents might maintain food supplies to their offspring at the expense of their own future survival. Thus, evidence that the declines of several granivorous species are associated with reductions in the survival rate of full-grown birds [72] could reflect increased costs of reproduction as well as any deterioration in seed supplies outside the breeding season.

In summary, providing a diversity of habitat provides for a diversity of organisms to exploit that habitat. Perhaps many of the wildlife benefits associated with organic farming are more associated with stimulating heterogeneity in farming practices and in resultant habitat structure as they are with the lack of chemicals *per se* [15,36,44,56]. As the intensification of farming has largely increased uniformity and reduced heterogeneity, there is perhaps a causal link between this aspect of intensification and the decline in farmland birds; mediated by loss of nesting habitat and reduction in food, and the spatial and temporal associations between these key resources [10,73,74].

Temporal variability

Different organisms have different habitat requirements (space, food or shelter), which are likely to change over time. Conceivably, one can imagine organisms that have sequentially changing requirements, such that an environment that is spatially uniform at any one time will fulfill their needs as long as it varies over time in the appropriate way. Therefore, in principle, the needs of a species can be fulfilled in two ways: (1) by moving between different habitats as they are required; or (2) by different habitats becoming available at the right time (in which case, spatial heterogeneity might be of less importance). We therefore need to consider how spatial and temporal variation interact. As well as modern agricultural practice inducing spatial uniformity (Table 1), it also induces temporal uniformity (Table 2). This is principally because the season during which land is productive has been extended, and the periods when the land is not in use are reduced. The efficiency of machinery also promotes a large-scale synchrony in management (Table 2), which reduces the spatial heterogeneity between fields.

Temporal variability arises from predictable processes, such as seasonality, and stochastic processes, such as the weather. Spatial variability acts to buffer temporal variation in resources, providing fallback habitats that might not be exploited in situations that are more favourable. The importance of temporal variation, and thus requirement for spatial heterogeneity, will depend on the life history of the organism (short-lived organisms are most vulnerable to variation), and the season in which resources might become limiting (in general, reproduction limited by food availability has less impact on population size than does winter-survival limited by food availability) [75].

Responding to heterogeneity

From individual-level processes to population responses

In previous sections, we have discussed the empirical findings that suggest that habitat heterogeneity at multiple spatial scales will be beneficial to biodiversity. We turn now to the issue of assessing how organisms might respond to the heterogeneity, and argue that this response should be assessed at a large-spatial scale.

Individuals need resources, and the resources available determine their life history, and hence contribute to the local population dynamics [76]. However, population performance might not reflect individual performance. For example, if territories are limiting, increasing productivity will not increase the population size. Large-scale population processes, such as dispersal, will also influence local population dynamics so consideration of what is good for specific species should include consideration of a range of scales. Baillie *et al.* [77] point out that dispersal could be detrimental to the population as a whole, because animals might disperse into poor-quality habitat. Because populations in such habitat are more likely to become extinct [78], dispersal might lead to a reduced population size and range contraction.

The benefit of any one habitat type is likely to be frequency dependent at the regional population level. For example, the sign of the association between numbers of several farmland bird species and arable land depends on the proportion of arable land in a region [39]. This scale dependence is important and, as most intensive studies are conducted in very local areas, extrapolations from local to regional populations should be made with caution. This is perhaps pertinent to assessing agri–environment schemes. A recent study of Dutch agri–environment schemes concluded that they had little effect on bird populations, assessed within a very small area [79]. Had the researchers assessed bird populations more broadly, it is possible that they might have found population-level effects, as has been shown for the response of cirl buntings *Emberiza cirlus*, corncrakes *Crex crex* and stone curlews *Burhinus oedicnemus* to targeted agri–environment scheme measures in the UK [23].

The way ahead

Habitat heterogeneity, at a range of spatial scales, has been greatly reduced wherever intensification has affected agricultural landscapes (Tables 1,2), and is clearly important in maintaining biodiversity within these landscapes by providing resources throughout the year for species-rich communities of organisms. Recognition that there has been erosion of heterogeneity at multiple spatial and temporal scales as a consequence of agricultural intensification can help to unify the response of conservation management because all agricultural practices (including agrochemical usage, cultivation practices, rotation planning and management of noncrop habitats) can, in principle, be tailored and targeted to increase rather than eliminate heterogeneity. Currently, European agri–environment scheme prescriptions do not focus explicitly on the creation and management of heterogeneity on farmland. For example, many of the management prescriptions available under the Rural Stewardship Scheme in Scotland will have the effect of enhancing habitat heterogeneity, but, in most cases, this is not stated explicitly as an aim [80]. Future debates about the biodiversity merits of new techniques (e.g. crops genetically modified or biomass crops) and management options might profitably consider whether they could be used to improve rather than diminish habitat heterogeneity.

We suggest that reversing declines in farmland biodiversity will require enhancing heterogeneity of farmland from within individual fields to whole landscapes. In principle, this is a hypothesis testable by experiment: is heterogeneity important more than the practices used to create it? From the management perspective, enhancing heterogeneity is easier both logistically and politically at smaller spatial scales. Indeed, many current agri–environment initiatives operate at the farm level. However, the impact of the resulting landscape-scale distribution of habitat patches on their effectiveness remains largely unknown. A recent UK policy review recommended the development of so-called 'broad and shallow' agri–environment options; low cost, low maintenance options, such as grass field margins or in-field strips, to ensure that some form of agri–environment management is spread widely across the UK landscape [81]. At the very least, approaches similar to this will increase habitat heterogeneity at the farm and/or field scale over a large percentage of farmland. However, it is important that the distribution of this management at the landscape scale is designed to maximize its effectiveness in reversing declines and range contractions of farmland wildlife. If this can be achieved then the problem of favouring management for some taxa at the expense of other is also mitigated; Part and Soderstrom [82] indicate that the requirements of plants and birds differ, but if the environment is sufficiently heterogeneous at all spatial scales, different taxa will find their own habitats.

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