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Does invasion by an alien plant species affect the soil seed bank?

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Abstract

Questions: How does invasion affect old-field seed bank species richness, composition and density? How consistent are these effects across sites? Does the soil seed bank match vegetation structure in old-fields?

Location: Menorca, Balearic Islands, Spain, western Mediterranean basin.

Methods: We monitored seed germination in soils from old-fields that were both uninvaded and invaded (legacy effect) by the annual geophyte *Oxalis pes-caprae*. We also added *O. pes-caprae* bulbs to uninvaded soils to test *O. pes-caprae* interference with seedling emergence (competitive effect). We compared species composition in the seed bank with that of the vegetation.

Results: Species richness in the seed bank and in the vegetation was not significantly different between invaded and uninvaded areas. Uninvaded areas did not have larger seed banks than invaded areas. More seedlings, especially of geophytes, emerged when *O. pes-caprae* bulbs were added to the soil. Species similarity between invaded and uninvaded areas was higher in the seed bank (74%) than in the vegetation (49%). Differences in species composition were as important as differences among sites. The degree of species similarity between the seed bank and the vegetation was very low (17%).

Conclusions: Despite invasion by *O. pes-caprae* not affecting species richness, the variation in the seed bank species composition in invaded and uninvaded areas, and the differences between the seed bank and the mature vegetation, highlights that even if the invader could be eradicated the vegetation could not be restored back to the exact composition as found in uninvaded areas.

Keywords: Bulb; Invader; Mediterranean community, Menorca, Non-native plant; *Oxalis pes-caprae*; Old-field; Regeneration; Seedling diversity.

Nomenclature: De Bolòs et al. (1990).

Abbreviation: MDS = Multidimensional Scaling.

Introduction

Biological invasions by alien plants can have devastating impacts on populations, communities and ecosystems (Parker et al. 1999; Levine et al. 2003). Consequently, interest in the processes influencing the invasion of natural systems and detailed examples of their impact has surged. Most studies evaluating the effect of plant invasions on biodiversity compare the effect of the presence of the invader on species composition and structure (Levine et al. 2003).

However, above-ground species diversity is only part of plant diversity (Margalef 2002). The seed bank is the total biodiversity reservoir reflecting past ecological conditions (Aparicio & Guisande 1997), offering potential for regeneration if the invader could be controlled or eliminated (Richardson et al. 1989; Reichard 1997; Dunbar & Facelli 1999). Invasion can cause disruption of seed inputs and consequently decrease species diversity of the seed bank. Plants co-existing with a dense cover of an invader may produce fewer seeds, die prematurely or even not establish at all, having a legacy effect especially if the seed bank is transient. Nevertheless, to date, few studies have investigated soil seed bank changes under invaded stands (but see Holmes & Cowling 1997; Standish et al. 2001; Holmes 2002).

Mediterranean regions of the world are highly invaded with alien plant species (Groves & di Castri 1991). Mediterranean basin ecosystems are also subjected to major land-use changes, such as extensive agricultural land abandonment, which create open sites for plant invaders to establish (Domènech et al. 2005). Although in general, old-fields are not perceived as having high conservation value, a unique element of Mediterranean biodiversity is represented in these disturbed, often ruderal, habitats. Many endemic and vulnerable plant species from arable land occur in these habitats and could represent the elements of the Mediterranean flora most at risk from invasions (Verlaque et al. 2001).

Oxalis pes-caprae is a South African annual geophyte which is currently invading many habitats of the Balearic Islands such as old-fields, pastures, tree groves and ruderal areas (Gimeno et al. 2006). *O. pes-caprae* often forms dense mats which cover the soil surface. Thus it is probably very successful at competing for light and space, excluding native plants as well preventing the deposit of seeds into the soil (Brooks 2001). The seed rain is likely to be reduced as this invader outcompetes the native vegetation, directly in the case of species with local dispersal. In addition, there could be indirect competition for bird dispersed species as large perennial herbs or shrubs acting as perches become rare in the presence of the invader. Like any dominant species, *O. pes-caprae* invasion could have an immediate competitive effect by reducing seedling emergence mainly due to shading and also a legacy effect by decreasing the soil seed bank due to cumulative interference through time. The aims of this study are (1) to investigate the competitive and legacy effect of *O. pes-caprae* on the seed bank of old-fields in Menorca (Balearic Islands), (2) to assess the importance of the soil seed bank in determining vegetation composition in uninvaded and invaded old-fields and (3) to evaluate the consistency of these effects across sites. We hypothesise that the soil seed bank is more affected by the *O. pes-caprae* cumulative effect (legacy effect) than by the immediate effect (competitive effect) of invasion.

Methods

Study species

O. pes-caprae (*Oxalidaceae*) has invaded several ecosystem types of the Mediterranean basin, Portugal, southwest England, California, Florida, Australia, India and New Zealand (Peirce 1997). It was first seen in the Mediterranean basin in 1796, reaching mainland Spain by 1825 and the Balearic Islands by 1870 (D'Austria 1884). *O. pes-caprae* leaves grow in a dense basal rosette, are long stalked with three cordate leaflets. The tendency for some alien plants to have this growth form overcomes the resistance to invasion by the established vegetation (Sanz-Elorza et al. 2005).

In the invaded range *O. pes-caprae* does not produce seeds, reproducing by means of bulbs (Rottenberg & Parker 2004). A single plant can produce between 10 and 40 bulbs (Vilà & Gimeno 2006). Plant development starts in autumn and finishes at the end of spring, after which bulbs remain dormant. This phenology, winter growth and spring senescence, could interfere with some plant functional groups, such as geophytes that emerge in early spring, hemicryptophytes that have leaves that stay close to the soil in winter and therophytes that recruit in autumn and winter.

Site description

The study was conducted in old-fields located in Menorca, Balearic Islands (40º05'39" and 38º38'25" N and 1º11'16" and 4º19'38" E). Menorca has a Mediterranean climate with an estimated mean annual precipitation of 642 mm and mean annual temperature of 19°C (http://www.caib.es). Study sites had calcareous stony soils (i.e. sandy clay loam texture with pH values ranging between 7.0 and 8.5).

In September 2002 we selected three old-fields that were at least 10 km apart. The selected fields were dominated by short grasses and herbs with scattered sclerophilous shrubs such as *Pistacea lentiscus* (*Anacardiaceae*) and *Phylleria angustifolia* (*Oleaceae*) and the geophyte *Asphodelus aestivus* (*Liliaceae*) (App. 2). Native species may have colonized the abandoned fields from the seed bank and as seed dispersed from adjacent shrublands.

These old-fields had both invaded and uninvaded patches. The mean size of the invaded patches was (± SE) 6.26 ± 1.14 m^2 and cover of *O. pes-caprae* was 70 ± 5.2%. There is no documented information about how long these old-fields have been abandoned and invaded. However, local farmers told us that these fields had not been planted with any cereal for at least eight years and recognized that fields were invaded even before agriculture abandonment. Currently, these old-fields are grazed and disturbed by cattle trampling.

Data collection

Sampling was conducted in autumn after seed rain to capture both the transient and persistent soil seed bank. In each of the three old-fields we sampled soils from eight randomly located 4-m^2 plots within the invaded area and 16 randomly located 4-m^2 plots within the uninvaded area. Each soil sample comprised 20 soil cores of 5 cm diameter and 5 cm depth (i.e. 480 cores total) randomly located within the 4 m^2 plot. For each plot, samples were manually bulked, mixed, dried at room temperature (20ºC) and large material (i.e. stones, root fragments) was removed.

We spread 500 g of each soil sample in a 5-mm layer on top of sterilized compost in 50 cm × 40 cm aluminium trays. In samples from invaded areas we manually removed the *O. pes-caprae* bulbs to test the legacy effect of *O. pes-caprae* invasion on the seed bank. Of the 16 soil samples from uninvaded areas, we took eight samples to which we added nine *O. pes-caprae* bulbs in each tray to test the immediate, competitive effect due to the interference of *O. pes-caprae* on seed germination. The number of bulbs added corresponds to the mean density of bulbs removed from the samples from invaded areas in the same sites. The remaining eight samples were not modified and were used as uninvaded controls. The experiment was performed outdoors at the Universitat Autònoma de Barcelona campus. We protected the trays with a mesh to avoid tray contamination by airborne seeds. We had five trays with sterile substrate to determine whether seed contamination was an issue. We maintained the trays with adequate moisture throughout the experiment.

We surveyed seed germination and seedling emergence over 12 months. We identified, counted and removed seedlings from the trays as they emerged except for *O. pes-caprae* in the competitive effect treatment. Each species was classified according to the Raunkiær (1934) growth forms: chamephytes (short shrubs), geophytes (herbs with underground reserve organs), hemicryptophytes (perennial herbs and grasses), phanerophytes (large shrubs and trees) and therophytes (annuals reproducing by seeds). Any species that could not be identified at the seedling stage were transplanted into separate pots and grown in unfertilized soil until identification was possible.

In spring 2003, the established vegetation in each site was also sampled from invaded and adjacent uninvaded areas. In each invaded and uninvaded area we located eight new 2 m × 2 m plots. The identity and number of species and corresponding growth forms were recorded in each plot.

Data analysis

To test for differences in species richness, number of growth forms and number of seedlings per tray we applied an ANOVA with the invasion treatment (i.e. competitive effect, legacy effect and uninvaded) as a fixed factor and the site as a random factor. Differences between invasion treatments, if significant, were compared with a Scheffé test. Differences in the vegetation between invaded and uninvaded plots in species and growth form richness were also tested with an ANOVA. Data were transformed if needed to meet the assumptions of parametric analysis.

To evaluate the similarity in species composition between treatments for the seed bank and in the vegetation, we used the Sørensen index calculated as $IS = (2C / A + B) \times 100$ where A and B are the number of species in each treatment and C is the number of species common to both treatments (Henderson 2003). The Sørensen index was also used to evaluate the similarity of species composition between the seed bank and the established vegetation.

In order to further detect similarities between treatments and sites while accounting for the relative abundance of different species, similarity in species abundance between all pairs of plots within the seed bank and within the vegetation was calculated with the proportional similarity index as

$$S = 1 - 0.5 \times SIp_x - p_yI \qquad (1)$$

where p_x and p_y are the frequency of each species in plots x and y respectively. The relative frequency of species in each site in the seed bank was calculated as the relative abundance of seedlings for each species, and in the vegetation as the relative cover of each species. The resulting pair-wise indices were used as input for a Non-metric Multidimensional Scaling ordination (MDS), an ordination technique useful for representing multivariate data in two dimensions (Legendre & Legendre 1998). All analyses were performed with STATISTICA (Anon. 2001).

Results

Effects of O. pes-caprae invasion on the soil seed bank

We found 104 different species in the seed bank belonging to 20 different families. The dominant plant families were: *Leguminosae* (18 species), *Gramineae* (16 species) and *Compositae* (10 species). The most common grass was *Lolium rigidum* and the most common herb *Anagallis arvensis* (*Primulaceae*) (App. 1). The number of species ranged from 14 and 21 species/tray and was significantly different between sites but not between treatments (Table 1, Fig. 1A). The number of seedlings varied from 50 to 250 seedlings/tray and they were significantly different among sites and invasion treatments (Table 1, Fig. 1B). Generally, more seedlings emerged in the competitive effect treatment (Scheffé

Table 1. ANOVA of the effect of invasion by *Oxalis pes-caprae* on the number of species, number of seedlings and number of growth forms /tray in the seed bank in Menorca (Balearic Islands).

Source of variation		Species richness		Growth forms		No seedlings	
	df	MS	*p*	MS	*p*	MS	*p*
Site	2	90.13	0.006	8.72	0.000	190372	0.000
Invasion	2	20.17	0.30	4.51	0.000	51826	0.003
Invasion × site	4	14.29	0.49	0.27	0.32	31355	0.008

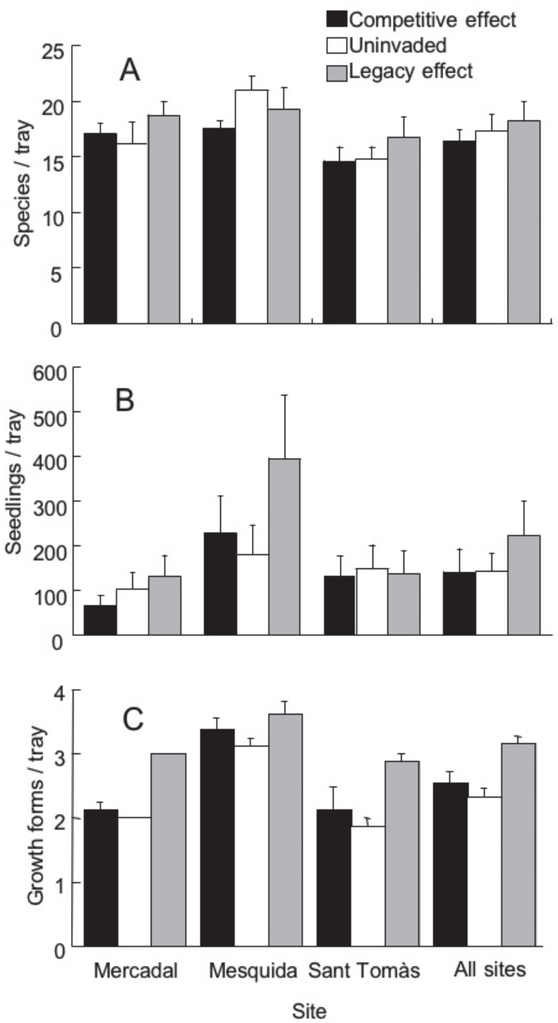

Fig. 1. (**A**) Species richness, (**B**) number of seedlings and (**C**) growth forms (mean + SE) in soil samples with different *Oxalis pes-caprae* invasion treatments for each site and in all sites in Menorca (Balearic Islands).

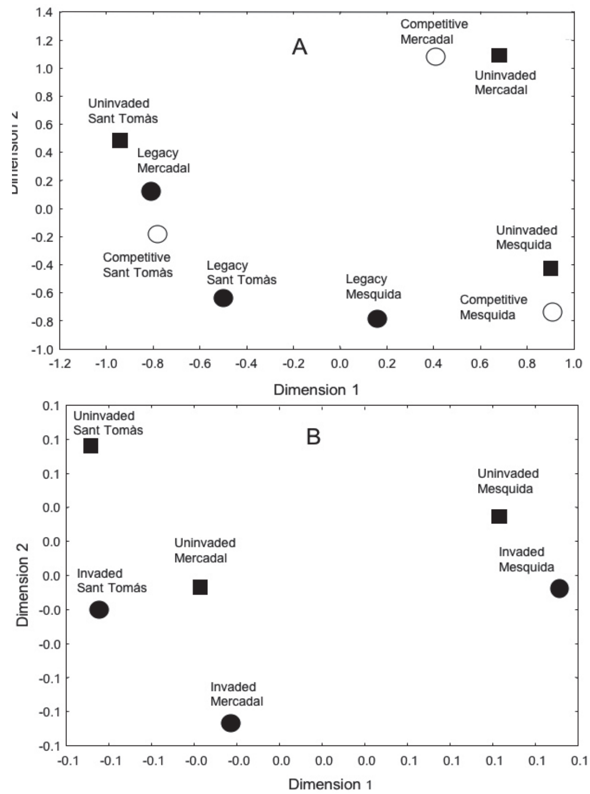

Fig. 2. Reduced-space plot of first two co-ordinates resulting from Non-metric Multidimensional Scaling (MDS) in uninvaded and *Oxalis pes-caprae* invaded plots in Menorca (Balearic Islands for (**A**) the seed bank and (**B**) the vegetation. See Methods for detailed description of treatments.

test, $p = 0.01$). However, the interaction invasion × site was significant, indicating that the effect of the invasion treatment differed between sites.

The species similarity of the seed bank between uninvaded soil samples and soil samples with an invasion legacy effect was ca. (± SE) 74.46 ± 2.66%. MDS revealed that the species composition in the seed bank in the legacy treatment was more distinctly separated from the uninvaded treatment than the competitive treatment (Fig. 2). However, MDS suggested that the identity and abundance of species in the seed bank is more dependent on the site than on the invasion treatment.

Total number of growth forms ranged from two to four per site and there were significant differences among invasion treatments (Table 1, Fig. 1C). As for species richness, more growth forms emerged in the competitive effect treatment (Scheffé test, $p < 0.0001$). Differences among sites were also significant with more growth forms in Mesquida (Fig. 1C). Therophytes were the most common growth form in all soil samples (from 60 to 100 % of seedlings) followed by hemicryptophytes (14.16 ± 0.98%), chamaephytes (3.17 ± 0.56%) and geophytes (1.56 ± 0.39%) (Fig. 3). Geophyte seedlings were more common in the competitive and legacy effect plots and absent in uninvaded plots (Fig. 3).

Effects of O. pes-caprae invasion on the vegetation

The vegetation comprised 115 species belonging to 37 families. The families with more species were: *Gramineae* (22 species), *Leguminosae* (20 species) and *Compositae* (13 species). Species richness was variable ranging from seven to 36 species/plot. The most common grasses were *Brachypodium distachyon* and *Dactylis glomerata*. The herbs *Daucus carota* ssp. *carota* (*Umbelliferae*) and *Anagallis arvensis* (*Primulaceae*) were also abundant (App. 2).

There was no significant difference in species rich-

Table 2. ANOVA of the effect of invasion by *Oxalis pes-caprae* on the number of species and number of growth forms in the vegetation in Menorca (Balearic Islands).

Source of variation	*df*	Species richness		Growth forms	
		MS	*p*	MS	*p*
Site	2	28.29	0.55	0.12	0.66
Invasion	1	10.67	0.63	0.04	0.71
Invasion × site	2	34.29	0.48	0.04	0.87

ness or growth form between invaded and uninvaded plots and between sites (Table 2). The species similarity between invaded and uninvaded plots was lower than for the seed bank, mean value was 49.15 ± 5.55 % (*n* = 3). For the seed bank, MDS also suggested that the identity and abundance of species in the vegetation is more dependent on the site than on invasion (Fig. 2).

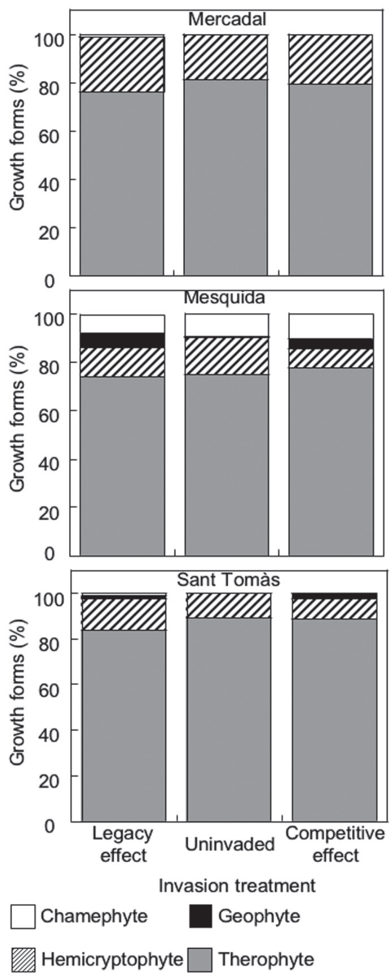

Fig. 3. Percentage of seedlings within different growth forms in the seed bank in different *Oxalis pes-caprae* invasion treatments for each site in Menorca (Balearic Islands).

The number of species found in each growth form was highest for the group of therophytes, ranging from four to 12 species and hemicryptophytes ranging from three to six species. It was lowest for the group of geophytes (from one to two species only).

Similarities between the vegetation and the seed bank

The number of plant species was similar in the established vegetation (115) to that in the soil seed bank (104). There was little similarity, however, between the composition of established vegetation and that of the soil seed bank in both invaded (16.79 ± 2.33%) and uninvaded (17.36 ± 0.74%) plots. Some species, mainly therophytes, that were very abundant in the vegetation, were also very abundant in the seed bank (e.g. *Anagallis arvensis* (*Primulaceae*), *Dactylis glomerata* (*Gramineae*), *Daucus carota* (*Umbelliferae*), *Medicago* spp. (*Leguminosae*) and *Linum strictum* ssp. *carota* (*Linaceae*). These species are early successional species considered weeds in agricultural Mediterranean lowlands, fallows and recently abandoned cereal crop fields (Folch 1986). However, 64 species present in the vegetation were absent from the seed bank and 19 species occurring in the seed bank were absent in the established vegetation. The number of families was almost twice as high in the established vegetation as in the soil seed bank. Likewise, the number of growth forms was higher in the established vegetation than in the seed bank. There were 22 annual species and 42 perennial species occurring only in the vegetation. In contrast, the seed bank had 48 annual species, 73% of which were also present in the vegetation, and 19 perennial species (68% also in the established vegetation).

Discussion

Our results do not confirm our hypothesis that the soil seed bank is more affected by the *O. pes-caprae* cumulative effect (legacy effect) than by the immediate effect (competitive effect) of invasion. In fact, we found a low legacy effect in species richness, growth form and density of the seed bank; on the contrary, *O. pes-caprae* had a facilitative effect in increasing seedlings emerging from the seed bank. Probably, in the short-term, the presence of *O. pes-caprae* may improve some micro-environmental conditions favouring seedling emergence by increasing soil phosphorus via the production and release of oxalates in the soil (Cannon et al. 1995). Besides amelioration of soil properties, shading by *O. pes-caprae* could also increase seedling recruitment of native species. Controlled experiments manipulating soil P and light would disentangle whether these two factors contribute to early seedling emergence of native species under an *O. pes-caprae* canopy.

Despite minor legacy seed bank effects of *O. pes-caprae* on species and growth form richness, species composition differed between uninvaded and legacy treatments. Almost 25% of the species present in uninvaded plots were absent in the legacy plots and relative abundance of species also changed as a result of the invader (e.g. geophytes were more abundant in legacy plots). However, consistent differences in seed bank species composition were overshadowed by compositional differences among sites. *O. pes-caprae* is an early seasonal species and contrary to our expectations it does not appear to significantly decrease seed production of neighbouring native species or interfere with seed rain from neighbouring plants. To test this assumption, the effect of the invader on the various stages of reproduction (i.e. from seed production to seedling establishment) of native species should be investigated, with special attention to how the presence of *O. pes-caprae* interferes with the native seed rain reaching the soil.

O. pes-caprae effects on the seed bank were site specific. Temporal and spatial variability in the structure of the seed bank is the norm as demonstrated by successional, seasonal and environmental gradient differences (Thompson 1978; Henderson et al. 1988; Houle & Phillips 1988; Peco et al. 1998a). In our study, the spatial variability of the seed bank structure is inherent to the nature of the habitat studied. These old-fields have a high plant diversity especially of early successional annuals with very idiosyncratic recruitment. These site variation effects imply that we can not generalize on the impacts of *O. pes-caprae* as has been found for the effects on vegetation structure across Mediterranean islands (Vilà et al. 2006).

We did not observe a decrease in species diversity with invasion as have other studies (Levine et al. 2003). Our results match previous vegetation surveys across Mediterranean basin islands in which this invader had a low effect on native species richness (Vilà et al. 2006). However, differences in species composition with *O. pes-caprae* invasion were more apparent in the vegetation than the seed bank suggesting that some species might germinate in invaded areas but not reach maturity (Holmes & Cowling 1997). Invaded plots tended to have fewer chamaephytes (i.e. short shrubs) and more geophytes than uninvaded plots.

The similarity between the composition of the seed bank and that of the vegetation was low, as found in the majority of studies comparing plant composition with seed bank composition (Díaz-Villa et al. 2003). The viable seed bank and the vegetation on a site are dynamically linked although some species may be present in one compartment but not the other (Thompson & Grime 1979). In our case, this low similarity was due to higher family richness, more species within growth forms and the presence of shrubs and trees in the vegetation but not in the seed bank. This finding reiterates that the seed bank is a poor predictor of vegetation composition and structure especially in old-fields (Warr et al. 1993; Holmes & Cowling 1997; Funes et al. 2003). Our results contrast with the high degree of association between the composition of seed banks and that of the standing vegetation in other Mediterranean ecosystems such as pastures (Levassor et al. 1990), grasslands (Peco et al. 1998b) and the chaparral (Parker & Kelly 1989) or in disturbed communities generally (Henderson et al. 1988; Marañón 1985; Ungar & Woodell 1993).

As it has been shown in other species, even if an invader might not change species richness it might alter successional pathways (Williams et al. 2003). Overall, the variation in the seed bank species composition in areas invaded and uninvaded with *O. pes-caprae*, and the differences between the seed bank and the mature vegetation highlights that even if the invader could be eradicated, the vegetation could not be restored back to the exact floristic composition of uninvaded areas.

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