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Short communication

# Environmental effects related to the local absence of exotic fish

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ABSTRACT

Given the extent of biological invasions in industrialized countries, our understanding of the determinants of overall patterns of biological invasions could gain most from consideration of why exotic species are absent from some areas, rather than from distribution patterns of exotic species. Fish communities were sampled at 381 sites representing 221 rivers in the Adour-Garonne stream system (116 000 km$^2$, SW France). Very few rivers were not colonized by exotic fish species, however, on a local basis, only 33% of the sampling sites hosted exotics. Using General Linear Modelling, we found that patterns of exotic fish (occurrence, number of species, proportion within assemblage) responded to both land-use and physical variables, whereas patterns of native fish only responded to the local meso-scale characteristics of each stream reach from headwaters to mouth. All fish communities were susceptible to invasion regardless of native species richness, and higher native species richness did not decrease the opportunity for establishment by exotic species. The likelihood that exotic fish are absent primarily increased with elevation and with lower human influence upon the land cover, while human-impacted landscapes (agricultural and urban areas) were more likely to host exotic fish and higher numbers of exotic species. In light of urban and agricultural development, our ability to detect responses of exotic species to landscape alterations using a combination of simple physical and land cover variables exemplifies a cost-effective technique for assessing areas at greater invasion risk in large stream systems.


## 1. Introduction

Introductions and invasions of alien species (including plants and animals) are a long-recognized problem (Vitousek et al., 1996; Lake and Leishman, 2004), and our ability to demonstrate statistical patterns of invasion by exotic species has often been seen as a key to the success of future conservation and management projects (Leung et al., 2004). Specifically, much effort has been directed towards predicting habitat susceptibility to invasion, and forecasting locations at greatest risk of invasions (Céréghino et al., 2005; Holway, 2005). However, given the extent of biological invasions in industrialized countries, our understanding of the determinants of overall patterns of biological invasions may now gain most from consideration of why exotic species are absent from some areas, rather than from consideration of the distributions of exotic species.

Fresh waters are the recipient of many exotic species (Moyle and Light, 1996) and the most frequently introduced freshwater organisms worldwide are fishes (Gozlan, 2008; Leprieur et al., 2008). Streams in particular have little immunity to exotic fishes (Morton, 1997), typically introduced to enhance recreational fishing and aquaculture, or for culinary and aquarist purposes or even to reduce pest insects (Keith and Allardi, 2001). Certainly due to fishing and/or economic concerns, their negative ecological effects (from the individual to the ecosystem level) are well documented (e.g. Townsend, 2003; Koehn, 2004), although some recent studies argued for negligible effects or even benefits for biodiversity (i.e. Gozlan, 2008). Fish introductions in rivers are described since the Roman era (Balon, 1995), and intensified during the 19th century (Allardi, 1984; Keith and Allardi, 1997). Surprisingly, some areas are still free of exotic fish (i.e. Sedell et al., 1990) and seem to harbor relatively "pristine" conditions, in terms of species assemblage. This situation raises new questions about the factors that prevented, and still prevent, biological invasions in such areas.

In this study, we focussed on the Adour-Garonne stream system (SW France), which drainage basin is subjected to urbanization and extensive agriculture. Assuming that increasing anthropogenic impact increases the chances of successful dispersal and invasion by exotic fishes (Lodge, 1993), we hypothesized that exotic and native species would differ in their responses to physical (e.g. elevation, stream order, distance from source, reach slope, air temperature) and land-use (e.g. urbanization, agriculture) variables. We predicted that exotic species richness broadly decreases with eleva-

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tion as anthropogenic pressures decline and streams become smaller. Specifically, we sought to produce explicit models which allow us to understand the relationships between the location of sites within the stream system, and the degree to which fish communities have been invaded by exotic species.

## 2. Methods

### 2.1. Study area and data collection

The Adour-Garonne stream system (south-western France) has a 116 000 km$^2$ drainage basin. During the last decades, the basin and its rivers have been intensively studied for various ecological aspects; a thorough description of the system was given in Tockner et al. (2009). We selected 381 sampling sites (Fig. 1) ranging from 2 to 1800 m a.s.l., thus representing 221 streams from high mountain, plain, and coastal areas.

All sites were sampled once by electrofishing during low-flow periods between 2002 and 2007. Two-pass removal sampling was used whenever possible, by wading in smaller rivers and by boat in the larger ones. Forty eight fish species were found to occur in the Adour-Garonne basin (Table 1), among which 17 were exotic species (according to Keith and Allardi, 1997, 2001; Persat and Keith, 1997). The biological variables assigned to each site for this study were: the occurrence (presence or absence) of exotic species, percentage of exotic species, number of exotic species, and the number of native fish species.

For each site, a Geographic Information System (GIS, Mapinfo professional 7.8) was used to delineate a geographical buffer zone representing a 1000 m-radius centered on the site. This size is well suited to assign a land-cover influence to each site (see also Compin and Céréghino, 2007) and falls within that of the "Reach Buffer" sensu Allan (2004), i.e., a buffer of 100 m to several hundred meters in width on each bank and some hundreds of meters to a kilometer in length. Sampling sites were then characterized using six physical variables, and three land-cover variables intended to account for anthropogenic pressure. The physical variables were elevation above sea level (a.s.l., m), slope (‰), stream order, distance from the source (km), drainage basin area (km$^2$), and maximum air temperature in June (°C, i.e. the mean of maximum temperatures recorded by the French Meteorological Services in early summer during the whole sampling period). The three land-cover variables were percent area within a buffer zone covered by forest (areas occupied by forest and woodlands with native or exotic coniferous and/or deciduous trees; scrub and herbaceous vegetation associations), urban development (industrial, commercial and transport units; artificial and non-agricultural vegetated areas), and agricultural area (arable lands, permanent crops and pasture). Digital land cover information was obtained from the CORINE land-cover database for Europe (CLC, 2000, European Environment Agency http://www.eea.europa.eu/; see also Cruickshank and Tomlison, 1996). This database was generated from orthorectified satellite images and provides thematic GIS map layers including up to 44 land-cover classes with a mapping scale of 1:100 000. These nine variables

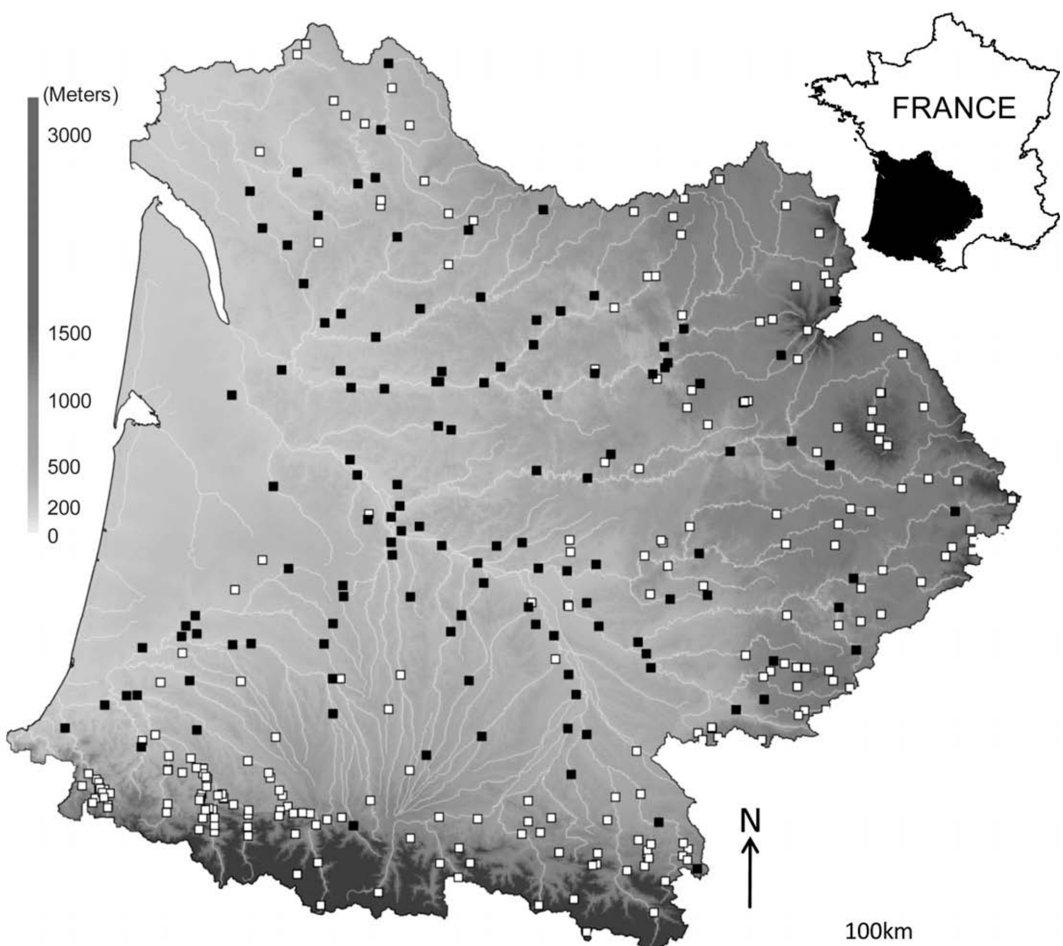


**Fig. 1.** The Adour-Garonne basin, and location of the 381 sampling sites. Filled squares denote locations where at least one exotic fish species was present, white squares denote locations where exotic fish are absent.

**Table 1**
List of the 48 fish species considered in this study with their status (N = native, E = exotic E) and their percentage of occurrence (number of sites where the species was found/total number of sites).

| Species | Status | Occurrence (%) |
|---|---|---|
| *Salmo trutta fario* | N | 0.63 |
| *Phoxinus phoxinus* | N | 0.60 |
| *Gobio gobio* | N | 0.59 |
| *Barbatula barbatula* | N | 0.49 |
| *Leuciscus cephalus* | N | 0.46 |
| *Rutilus rutilus* | N | 0.33 |
| *Anguilla anguilla* | N | 0.29 |
| *Barbus barbus* | N | 0.28 |
| *Alburnus alburnus* | N | 0.26 |
| *Lampetra planeri* | N | 0.20 |
| *Lepomis gibbosus* | E | 0.20 |
| *Perca fluviatilis* | N | 0.19 |
| *Leuciscus leuciscus* | N | 0.18 |
| *Salmo salar* | N | 0.17 |
| *Cottus gobio* | N | 0.14 |
| *Esox lucius* | N | 0.08 |
| *Chondrostoma taxostoma* | N | 0.08 |
| *Cyprinus carpio* | E | 0.08 |
| *Abramis brama* | N | 0.07 |
| *Carassius sp.* | E | 0.07 |
| *Silurus glanis* | E | 0.07 |
| *Tinca tinca* | N | 0.07 |
| *Ameiurus melas* | E | 0.06 |
| *Scardinius erythrophtalmus* | N | 0.06 |
| *Rhodeus amarus* | N | 0.06 |
| *Micropterus salmoides* | E | 0.06 |
| *Blicca bjoerkna* | N | 0.06 |
| *Gymnocephalus cernua* | E | 0.06 |
| *Onchorhynchus mikiss* | E | 0.04 |
| *Pseudorasbora parva* | E | 0.03 |
| *Sander lucioperca* | E | 0.03 |
| *Barbus meridionalis* | N | 0.03 |
| *Petromyzon marinus* | N | 0.03 |
| *Gasterosteus aculeatus* | N | 0.02 |
| *Pungitius pungitius* | N | 0.02 |
| *Gambusia affinis* | E | 0.02 |
| *Pachychilon pictus* | E | 0.02 |
| *Thymallus thymallus* | E | 0.01 |
| *Platichthys flesus* | N | 0.01 |
| *Hypophtalmichthys molitrix* | E | 0.01 |
| *Salvelinus fontinalis* | E | 0.01 |
| *Chelon labrosus* | N | 0.01 |
| *Leuciscus burdigalensis* | N | 0.01 |
| *Alburno bipunctatus* | E | <0.01 |
| *Leucaspius delineatus* | E | <0.01 |
| *Alosa alosa* | N | <0.01 |
| *Cobitis taenia* | N | <0.01 |
| *Leuciscus soufia* | N | <0.01 |

were chosen because they characterize the location of sampling sites within the stream system and within the regional landscape mosaic, and they are easy to describe using a GIS. The use of simple variables in a successful final model could thus reduce the effort and cost of data collection for water management applications.

### 2.2. Data analyses

To analyze the relationships between environmental variables and occurrence of exotic species, percentage of exotic species, number of exotic species, and the number of native fish species, we used Generalized Linear Modelling, including river basin as a random factor to control for the possible non-independence of sampling points coming from the same basin. When the dependent variable corresponded to count data (number of exotics or number of native species) we used Poisson distributed errors and the log link to fit the models. When the dependent variables corresponded to occurrence data or proportions (presence of exotics or number of exotics out of total number of fish species) we used binomial distributed errors and the logit link to fit the models. All analyses were done with the GLIMMIX procedure in SAS 9.2. (SAS Institute 2009). Models were fitted using Laplace approximation which is more accurate than Penalized quasilikelihood (Bolker et al., 2009), and based on likelihood. Significance of random effect was tested by likelihood ratio test using the covtest statement. Environmental variables were log transformed to fit a normal distribution (elevation, distance, slope and drainage area) or ranked when not normalized by usual transformations (temperature, % urban and % agricultural area); see Conover and Iman (1981). Stream order and number of native species fitted a normal distribution. As land-use was classified in three exclusive categories (% urban, agricultural and forest areas), a strong colinearity existed between the three variables. For this reason, only two of the categories were included in further analyses (% urban and % agricultural areas), but statistically significant relationships of the same sign for both variables must also be interpreted as a negative relationship for the third one.

## 3. Results

Fish were present in all sampling sites, with exotic species occurring at 129 sites out of 381. The examination of simple occurrence data of exotic fishes on a geographical map (Fig. 1) suggests that most headwater sites are depleted in exotic species compared to those sites located in plain areas. This is particularly true of the Pyrenees Mountains (south of the Adour-Garonne system) and the Massif Central Mountains (east of the system). However, the drainage basin, which is located in the northwestern plain area, is also devoid of exotic species. The variance explained by the exotic species occurrence model was 48.6%. The occurrence of exotic species was positively correlated with the number of native species ($p = 0.0004$; Table 2) and negatively correlated with elevation and slope ($p < 0.0001$ and $p = 0.007$, respectively). In other words, the likelihood that exotic species are locally absent increased with decreasing numbers of native species and increasing elevation. The proportion of exotic species within local assemblages was negatively correlated with slope and elevation ($p = 0.01$ and $p = 0.002$, respectively) and it was positively correlated with temperature, stream order, urbanization and agriculture ($p < 0.0001$, $p = 0.04$, $p = 0.02$ and $p = 0.02$, respectively). The proportion of exotic species decreased with elevation, but increased with temperature and anthropogenic factors.

The exotic fish richness model explained 38.5% of the total variance in numbers of exotic species. The number of exotic species was influenced both by natural factors and anthropogenic ones. Slope and elevation were negatively correlated with the number of exotic species ($p = 0.002$ and $p = 0.01$, respectively; Table 2). Temperature was positively correlated with exotic species richness ($p < 0.0001$), as well as urbanization ($p = 0.02$). By contrast, land-use variables did not correlate significantly with the number of native species, meaning that topographical zonation overcame the anthropogenic influence. The native fish richness model explained 23.6% of the total variance in numbers of native species. Slope and elevation were negatively correlated with the number of native species ($p < 0.0001$ and $p = 0.0003$, respectively), whereas temperature and distance from the source were positively correlated with native species richness ($p = 0.02$ and $p < 0.001$, respectively; Table 2).

## 4. Discussion

Throughout the world, environmental policies aiming at preserving the biological diversity of terrestrial and/or aquatic ecosystems heavily rely on action plans for the delineation of zones of

**Table 2**
Models analyzing the patterns of fish distributions using four biological indicators; occurrence and proportion of exotic fish species, number of native and exotic species. Only variables with $p < 0.05$ are interpreted as statistically significant. Deviance of the null models, dispersion values ($\Phi$ = deviance of the final model/degrees of freedom) and percentage of variance explained are given.

| | Effect | Estimate | $F$ | df | $p$ |
|---|---|---|---|---|---|
| Occurrence of exotic species | Elevation | −2.729 | 15.70 | 1.368 | <0.0001 |
| | Distance source | −0.513 | 0.22 | 1.368 | 0.64 |
| | Slope | −1.963 | 7.25 | 1.368 | 0.007 |
| | Drainage area | −0.745 | 0.95 | 1.368 | 0.33 |
| | Temperature | 0.016 | 0.28 | 1.368 | 0.59 |
| | Urbanization | 0.011 | 0.38 | 1.368 | 0.54 |
| | Agriculture | 0.006 | 1.30 | 1.368 | 0.26 |
| | Stream order | 0.594 | 3.57 | 1.368 | 0.06 |
| | Number of native species | 0.254 | 13.38 | 1.368 | 0.0003 |
| | Deviance | 250.65 | | | |
| | $\Phi$ | 0.97 | | | |
| | Variance explained | 48.6% | | | |
| Proportion of exotic species | Elevation | −0.518 | 10.17 | 1.369 | 0.002 |
| | Distance source | −0.347 | 0.59 | 1.369 | 0.44 |
| | Slope | −0.818 | 6.43 | 1.369 | 0.01 |
| | Drainage area | −0.200 | 0.45 | 1.369 | 0.50 |
| | Temperature | 0.084 | 33.82 | 1.369 | <0.0001 |
| | Urbanization | 0.016 | 5.38 | 1.369 | 0.02 |
| | Agriculture | 0.006 | 5.24 | 1.369 | 0.02 |
| | Stream order | 0.261 | 4.64 | 1.369 | 0.03 |
| | Deviance | 545.84 | | | |
| | $\Phi$ | 0.94 | | | |
| | Variance explained | 24.9% | | | |
| Number of native species | Elevation | −0.249 | 13.27 | 1.369 | 0.0003 |
| | Distance source | 0.662 | 27.07 | 1.369 | <0.0001 |
| | Slope | −0.428 | 23.67 | 1.369 | <0.0001 |
| | Drainage area | −0.102 | 1.11 | 1.369 | 0.29 |
| | Temperature | 0.007 | 5.04 | 1.369 | 0.03 |
| | Urbanization | −0.002 | 0.69 | 1.369 | 0.41 |
| | Agriculture | −0.001 | 2.53 | 1.369 | 0.11 |
| | Stream order | −0.069 | 2.70 | 1.369 | 0.10 |
| | Deviance | 1681.87 | | | |
| | $\Phi$ | 1.03 | | | |
| | Variance explained | 23.6% | | | |
| Number of exotic species | Elevation | −0.722 | 22.03 | 1.369 | <0.0001 |
| | Distance source | 0.238 | 0.36 | 1.369 | 0.55 |
| | Slope | −1.077 | 12.40 | 1.369 | 0.0005 |
| | Drainage area | −0.148 | 0.28 | 1.369 | 0.60 |
| | Temperature | 0.082 | 28.76 | 1.369 | <0.0001 |
| | Urbanization | 0.015 | 5.80 | 1.369 | 0.02 |
| | Agriculture | 0.004 | 3.26 | 1.369 | 0.07 |
| | Stream order | 0.103 | 0.78 | 1.369 | 0.38 |
| | Deviance | 653.73 | | | |
| | $\Phi$ | 1.12 | | | |
| | Variance explained | 38.5 | | | |

ecological interest (which concentrate rare and/or threatened species, or which have patrimonial values – see e.g., the Natura 2000 network of the European Union). Biological invasions often form part of such frameworks through more specific projects intended to enhance our theoretical knowledge of interactions between native and exotic species (e.g. Cucherousset et al., 2008a), and/or to propose practical decision tools for managers faced with sets of exotic species that generate local and/or regional nuisance. These policies therefore have an impact on a wide range of people and activities such as water consumers and recreational users, agriculture, industry and business activities. Environmental managers generally ask for explicit schemes such as distribution patterns that allow them to identify areas at greater ecological risk. If threats associated with economy-oriented projects align with zones deprived of exotic species, this could add new impetus to calls for freshwater conservation policies. Among the questions that are posed to the scientific experts, the most common ones are: (1) which areas within a regional system contain exotic species? and (2) which environmental variables explain the presence of exotic species? In the Adour-Garonne stream system (SW France), very few rivers were not colonized by exotic fish species. However, on a local basis, only 33% of the sampling sites hosted exotic fish species. Paradoxically, the local absence of exotic species in such invaded systems is thus more intriguing than the occurrences.

With a large number of explanatory variables, one may overfit the models so that they perform well in the context of the dataset used to generate them, but fail to be robust when used elsewhere (Rushton et al., 2004). The variance explained by our GLMs was about 48% for the exotic species occurrence model, and 38.5% for exotic species richness, although we used a limited number of variables. The variance explained by the native fish and proportion of exotic fish models was lower, but still about 24–25%. The suggested schemes are thus relevant, and should perform well in other areas. Our results showed that patterns of exotic fish (occurrence, number of species, proportion within assemblage) responded to both land-use and physical variables, whereas native fish responded to the gradient of physical characteristics of streams from headwaters to mouth. The species richness of native fish gradually increased from headwaters to plains as a result of downstream addition of species, suggesting that anthropogenic alterations of the riparian and watershed landscapes did not override geomorphological controls on the distribution of native fish (see Cucherousset et al. (2008b) for a detailed analysis of patterns for native fish in our study system). The likelihood that exotic fish are absent increased with elevation and reach slope, while the proportion of exotic species within assemblages decreased with decreasing urbanization and agriculture. The positive correlation between occurrence of exotic species and native species richness indicated that all communities were susceptible to invasion regardless of native species richness (see also Moyle and Light, 1996; Gido and Brown, 1999), and that higher native species richness did not decrease the opportunity for establishment by exotic species (Mack et al., 2000). The relationship between native species richness and invasion success is intensely debated. Some models suggest that species richness should limit the capacity of new species to establish in an area due to the saturation of the available niches (Elton, 1958; Case, 1990; Tilman, 1999; Kennedy et al., 2002). However, many observational studies suggest the opposite, the richness of native and exotic species being correlated (Gilbert and Lechowicz, 2005; Perelman et al., 2007) or, as in this study, exotics being present in the areas with greater native species richness.

Mountain streams may represent harsh environments which are physically stressful (higher river competence and erosive forces generated through the combination of slope with other variables such as water depth and current velocity, snowmelt floods, etc.), so that a smaller proportion of potential colonizers could become established (Gido and Brown, 1999). Some sites located in the plain, especially in the northwestern area of the watershed, presented very low proportions of exotic fish. However, we assume that these particular plain sites present lower opportunities for fish introduction because of the lower human influence in this sub-system (Tockner et al., 2009) (see below), rather than because of fast flowing and fluctuating environments.

Mountain sites are less subject to human influence, and have usually not been subjected to high levels of introductions. We found that the proportion of exotic species in the fish assemblage and the local numbers of exotic species were positively correlated with the extent of urbanization. According to our GLM results, this pattern did not result from drops in native species richness with increasing anthropogenic influence, but actually from increases in numbers of exotic species with urban development. Human-impacted landscapes (characterized here by higher proportions of urban and/or agricultural areas) are more likely to host exotic fish and higher numbers of exotic species (Leprieur et al., 2008), and this was true for the Adour-Garonne stream system. According to McKinney (2001), human population size is a good predictor of exotic fish species richness. Similar observations were reported for plants (Whitney, 1985), mammals (Hansen et al., 2005), and birds (Germaine et al., 1998; Donnelly and Marzluff, 2004). Therefore, both literature data and own our study support the conclusion that exotic species associated with humans predictably colonize ecosystems as agricultural and/or urban land cover increases.

In conclusion, whilst exotic species were predictably more likely to be absent from headwater streams subjected to low anthropogenic influence, we demonstrated that the number and proportion of exotic species responded to broad land-cover categories such as "agricultural area" and "urban area", and that the 1000 m-radius buffer zone adapted from Allan (2004) was appropriate to detect changes in number and proportion of exotic species in a large stream system. Since the challenge of recent applied research is to assess models having the broadest capability of predicting spatial patterns of community organization (including native and exotic species), we suggest that the combination of simple physical and land-cover variables obtained from thematic GIS map layers should be relevant to identify and to delineate areas of concern in integrated management of biological invasions at watershed levels. Moreover, our study implicitly supports the idea that action plans should be designed at a landscape scale (Ward, 1998). In light of urban and agricultural development, our ability to detect responses of exotic species to landscape alterations exemplifies a cost-effective technique for assessing areas at greater invasion risk in large stream systems.

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