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Birds are tracking climate warming, but not fast enough

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Range shifts of many species are now documented as a response to global warming. But whether these observed changes are occurring fast enough remains uncertain and hardly quantifiable. Here, we developed a simple framework to measure change in community composition in response to climate warming. This framework is based on a community temperature index (CTI) that directly reflects, for a given species assemblage, the balance between low- and high-temperature dwelling species. Using data from the French breeding bird survey, we first found a strong increase in CTI over the last two decades revealing that birds are rapidly tracking climate warming. This increase corresponds to a 91 km northward shift in bird community composition, which is much higher than previous estimates based on changes in species range edges. During the same period, temperature increase corresponds to a 273 km northward shift in temperature. Change in community composition was thus insufficient to keep up with temperature increase: birds are lagging approximately 182 km behind climate warming. Our method is applicable to any taxa with large-scale survey data, using either abundance or occurrence data. This approach can be further used to test whether different delays are found across groups or in different land-use contexts.

Keywords: birds; breeding bird survey; climate warming; community composition; global changes; range edges

1. INTRODUCTION

Climate change is now considered a major driving force of species declines and extinctions (Parmesan & Yohe 2003; Thomas *et al.* 2004; Thuiller *et al.* 2005a,b; Pounds *et al.* 2006; Sekercioglu *et al.* 2008). Biodiversity responses to climate warming have been documented through the study of changes in distributions (Hickling *et al.* 2006; Araújo & New 2007), abundances (Biro *et al.* 2007), phenologies of individual species (Barbraud & Weimerskirch 2006; Both *et al.* 2006; Sherry *et al.* 2007) or in more integrated measures such as species community richness and composition (Menéndez *et al.* 2006; Lemoine *et al.* 2007; Wilson *et al.* 2007).

Very detailed studies have shown that breeding adjustment to an advanced food peak was insufficient for some species (Both *et al.* 2006). Mistiming in phenology is population- and species dependent (Sherry *et al.* 2007), however, and suffers from a lack of generalization. Thus, assessing whether community changes are sufficient to cope with climate change has been hardly quantified (but see Menéndez *et al.* 2006). To measure whether communities are tracking climate warming fast enough, one can use a comparison between changes in species distribution predicted by climate warming and those observed with empirical data (Virrkala *et al.* 2008). Yet, such an estimate relies on (i) appropriate climate models predicting the climate-dependent distribution for many species and (ii) independent successive atlas studies with enough precision and comparable sampling effort at the margin of the species distribution.

Furthermore, it is likely that measuring changes in species' range edges only partly reflects the species responses to climate warming. Indeed, we expect that changes occurring within the core range of species distributions and those occurring at species' range edges are driven by different ecological mechanisms (Brown *et al.* 1996; Orme *et al.* 2006). Yet, investigating whether species are tracking climate warming fast enough within their range has never been investigated (but see Lenoir *et al.* 2008).

Here, we propose a framework to measure whether the observed changes in species' distributions are tracking climate warming fast enough to cope with temperature increase. This framework does not only focus on changes in species' range edges but rather reflect a species' response over its entire range. Moreover, this framework does not need any assumption about projection of future species distribution and does not heavily rely on the precision of distribution data.

First, for a given species, one can estimate the long-term average temperature experienced by individuals of that species over its range (species temperature index, STI). This measure is the simplest parameter of the species climate envelope, a concept used in most climate change investigations (Thuiller *et al.* 2005a,b; Hijmans & Graham 2006). Moreover, such a species-specific climate niche measure was shown to be powerful in predicting the long-term responses of breeding bird species to climate warming (Jiguet *et al.* 2007).

STI can be easily calculated for many species with widely used spatial distribution data based on abundance or presence-absence. Note that the STI of a given species is obviously scale dependent. For instance, a species' STI

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can be higher (or lower) if calculated within a subset of the species' range (depending on the average temperature of the subset considered) than if calculated over its entire range. Yet, if STIs are calculated for several species within the same area, the ordering of each species-specific STI among each other will always differentiate species according to the mean temperature at which they occur.

Then, any local species assemblage within the area of interest can be characterized by a community temperature index (CTI) calculated as the average of each individual's STI present in the assemblage. High CTI would thus reflect a large proportion of species with high STI, i.e. of more high-temperature dwelling species. The CTI can then be used to measure local changes in species composition. Indeed, if current climate warming favours high STI species compared with low STI species, CTI should increase locally.

Finally, such temporal changes in CTI may be easily interpreted as a northward shift, if projected on the existing south–north gradient in CTI. The same exercise may be done for temperature: any temporal change in local temperature may be projected on the existing south–north climatic gradient. The comparison of these two rates of change may tell us which of bird composition or temperature present the most rapid northward shift.

Here, we used data from 1514 plots from the French breeding bird survey (FBBS) scheme to measure the temporal trend of bird CTI between 1989 and 2006. We found that CTI has strongly increased during the period considered revealing a profound change in community composition. However, we found that in two decades, French birds have accumulated approximately a 182 ± 53 km lag in their response to climate warming.

2. MATERIAL AND METHODS

(a) *French breeding bird survey*

The FBBS was started in France in 1989 based on volunteer skilled ornithologists counting birds following a standardized protocol at the same plot for several years (Julliard & Jiguet 2002). In each plot, a given observer monitored 10 point counts separated by at least 200 m. All visible individuals and singers were counted on these permanent point counts for a fixed period of 5 min. To be validated, the count must be repeated on approximately the same date of the year (± 7 days within April to mid-June), the same time of the day (± 15 min within 1–4 hours after sunrise) and in the same order, by the same observer. A new sampling design was launched in spring 2001, for which surveyed plots were not freely chosen but selected randomly, ensuring that sampled habitats were representative: each observer provided a locality, and a 2×2 km plot to be prospected was randomly selected within a 10 km radius (i.e. among 80 possible plots). In each plot, the observer also monitored 10 point counts following the standardized protocol already mentioned. Such random selection ensures the survey of varied habitats across the whole country (including intensive farmlands, forests, suburbs and cities; figure 1).

(b) *Species temperature index*

For a given species, STI was obtained from the combination of data from the EBCC atlas of European breeding birds (Hagemejerr & Blair 1997) and the spatial distribution of the mean temperature (averaged for the period 1950–2000, from

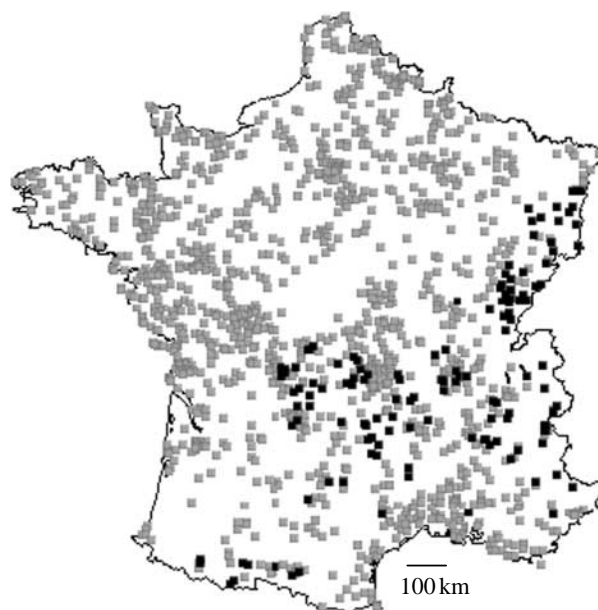


Figure 1. Spatial distribution of breeding bird survey plots. Each grey plot is a 2×2 km square (surveyed at least 2 years during 1989–2006 in which 10 point counts were evenly distributed). The CTI was calculated on each point count during the surveyed period. To estimate the south–north gradient in CTI, squares located above 800 m (in black) were excluded.

WorldClim database <http://www.worldclim.org>) of the bird breeding season (from March to August). Note that a given species can have a biased European STI compared to its true STI. For example, for a species that occurs from North Africa to northern Europe, averaging the temperature of the European atlas cells (i.e. excluding North Africa) would result, for that species, in a STI lower than its true value. Yet, this bias is true for each species and should not affect our analysis. Indeed, to further calculate the CTI, we are only interested in the relative species' STI rather than on the actual species' STI over its entire range. To illustrate this issue, we calculated each species' STI using the whole EBCC atlas coverage, and, separately, using only the French subset of the EBCC atlas. As temperature in France is, on average, warmer than the mean temperature of the whole of Europe, we found that the French STIs were higher than the European STIs (mean of the difference European minus French STI: -0.34°C , paired t -test: $p < 0.001$). Yet, both French and European STIs were highly correlated $R^2 = 44\%$; $p < 0.0001$). We are thus confident that STI can be safely used to discriminate species according to the temperature at which they occur although only subsets of the species ranges are considered.

(c) *Temporal trends and south–north gradients in CTI and temperature*

Each local species assemblage monitored by the FBBS was characterized by a CTI calculated as the average of each individual's STI present in the assemblage. The year-to-year temporal variations of CTI was then calculated with generalized linear model, using data from all monitored plots ($n = 1514$) between 1989 and 2006 (the year 2001 was fixed as a reference). In these models, the plots were considered as a fixed factor and year either as a continuous or categorical variable. Note that in such an additive model, the trend is not sensitive to the spatial location of FBBS plots. To test whether the temporal trend was robust to a change in

the quality of the data, the same model was also performed using CTI calculated on occurrence data (instead of abundance) from the FBBS. In this case, CTI was calculated as the average of each species' STI (not weighed by each species abundance) present in the assemblage.

We further estimated the rate of change in CTI from south to north. The south–north gradient of CTI was calculated using all plots monitored in 2005, the year with the maximum number of surveyed plots ($n=878$). We then excluded plots located above 800 m ($n=156$, figure 1), as we were interested in the south–north gradient of CTI and that this gradient would have been locally biased by plots located in high altitude (note that including these plots did not substantially change the results). We then estimated the slope of the regression between CTI and latitude using the remaining plots ($n=722$). To assess whether this slope was robust to change in data use, the south–north gradient in CTI was also estimated using presence–absence data from the French atlas (Yeatman-Berthelot & Jarry 1994) dataset ($n=201$ grid cells not located in mountains), which is totally independent from the FBBS.

Similarly, we estimated the temporal trend as well as the south–north gradient in March–August temperature. To estimate the trend in temperature over 1989–2006, we calculated, for each year, the average March–August temperature anomaly of the 5, 10, 15 or 20 preceding years. The anomalies are calculated using the average temperature of the period 1961–1990 as a reference (Brohan *et al.* 2006) and were obtained from the CRUTEM3 datasets (available at <http://www.hadobs.org>). We chose this moving window approach because we do not expect birds to respond to climate warming instantaneously but with an unknown delay corresponding to their demographic regulation.

The rate by which the average temperature increases from south to north over a given area depends on the period, the season and the land surface considered. For instance, in the Northern Hemisphere, the latitudinal gradient in annual temperature was estimated to be -0.556°C per 100 km over the last century (Jain *et al.* 1999). In our particular case, the latitudinal temperature gradient should be (i) limited to France, (ii) to the March–August period (birds are sampled during spring–summer), and (iii) to non-mountainous regions (which would negatively bias the south–north gradient locally). The latitudinal temperature gradient was thus provided by WorldClim by regressing temperature with latitude over the entire country (excluding plots located in mountains, i.e. approximately 800 m elevation).

Obviously, temperature is not only changing from south to north. But the longitudinal gradient of temperature was found to be negligible (we found that temperature significantly decreased from east to west by $0.047^{\circ}\text{C km}^{-1}$ but that this relation was very weak, $R^2=0.006$). Moreover, FBBS was inappropriate to track vertical distribution of birds so that we focused on latitudinal change in CTI or in temperature.

3. RESULTS

During 1989–2006, the CTI of French birds has increased steadily ($+0.0060 \pm 0.0007$ s.e. yr^{-1} ; $F_{1,16}=53.01$; $p<0.0001$; figure 2). This linear temporal trend, based on abundance data of the 105 most common terrestrial species (representing 99.5% of all individual birds recorded by the FBBS), accounted for an amazingly high amount of the total between-year variation in CTI

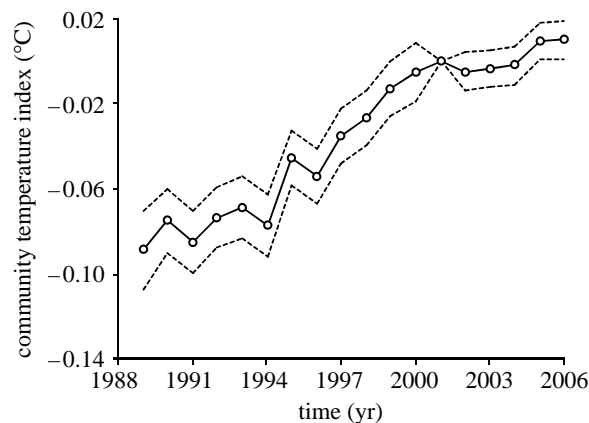


Figure 2. Temporal trend of the CTI. The CTI of a given species assemblage is the average of each STI weighed by species abundance. It was calculated for each year and on each point count monitored by the FBBS scheme during 1989–2006 for the 105 most common species. STI for a given species is the long-term average temperature experienced by breeding individuals of that species over its European range. Dashed lines represent standard error around the mean (s.e.).

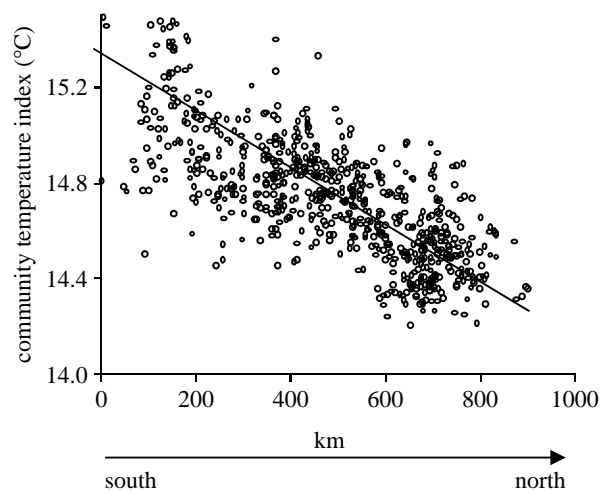


Figure 3. South–north gradient of the CTI. Each point represents the CTI of a breeding bird survey plot, monitored in 2005. For each plot ($n=722$), the CTI was calculated as the average of the CTI calculated in the 10 point counts of that plot. In a given point count, the CTI is the average of each STI of all individuals detected in that point count.

($R^2=93\%$). Moreover, the same relationship was found before and after 2001, when a random stratified sampling scheme was launched (the effect of change in the monitoring protocol on CTI trend: $F_{1,15}=0.03$; $p=0.94$). Using abundance data from the FBBS, we found that CTI was decreasing from south to north in France (-0.119 ± 0.004 s.e. unit of CTI per 100 km, $F_{1,720}=809$; $p<0.0001$; $R^2=53\%$; figure 3). During the period considered, the increase in CTI thus corresponds to a 91 ± 11 km northward shift in bird community composition.

Interestingly, a comparable shift was found using either presence–absence data or even data independent from the FBBS. Indeed, using presence–absence data, we found that during the 1989–2006 period, CTI (calculated as the average STI of all species, but not weighed by each species' abundance) of French birds also increased steadily ($+0.0044 \pm 0.0005$ s.e. yr^{-1} ; $F_{1,16}=35.46$; $p<0.0001$). The south–north gradient in CTI was also available using

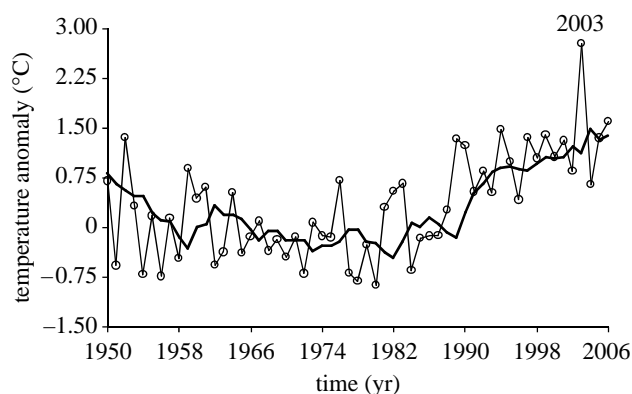


Figure 4. Temporal trend of the average March–August temperature anomaly in France from 1950 to 2006. For each year, the anomaly is calculated from the base period 1961–1990. The thick curve represents a 5 years moving window (the average temperature anomaly of the 5 preceding years). The year 2003 was the greatest anomaly for the period considered.

presence–absence data from the FBBS (-0.102 ± 0.003 s.e. unit of CTI per 100 km, $F_{1,720} = 748$; $p < 0.0001$; $R^2 = 51\%$) and suggest that the increase in CTI during 1989–2006 corresponds to a 77 ± 9 km northward shift in bird community composition. This shift is not different from the shift estimated with abundance data ($p > 0.05$). Similarly, the French breeding bird atlas provides an independent measure of the south–north gradient in CTI (-0.0906 ± 0.003 s.e. unit of CTI per 100 km, $F_{1,199} = 838$; $p < 0.0001$; $R^2 = 80\%$). Based on this gradient, and on the temporal trend in CTI estimated with presence–absence data, we found that bird community composition has shifted 87 ± 10 km northward (this estimate is not different from others, $p > 0.05$).

We then estimated the northward shift in temperature during the period 1989–2006 using the same reasoning. During 1989–2006, the temperature in France was much warmer than it used to be (Moisselin *et al.* 2002); the temporal trend of the temperature anomaly, averaged over 5 years was $+0.068^\circ\text{C} \pm 0.008$ s.e., $p < 0.0001$ (figure 4). This trend was not different using 5, 10, 15 or 20 years moving window (ANCOVA: $F_{3,64} = 1.19$; $p = 0.32$). Note that France experienced extreme warmth in 2003 ($+2.78^\circ\text{C}$ in temperature anomaly) compared with the period 1989–2006 (mean of anomaly temperature: $+1.16 \pm 0.5^\circ\text{C}$). We finally estimated that, in France, the March–August temperature is roughly decreasing from south to north by $0.45^\circ\text{C} \pm 0.07$ s.e. per 100 km (this trend can be reliably considered to be linear $p < 0.0001$, $R^2 = 75\%$). The temperature increase during 1989–2006 thus corresponds to a northward shift of $273 (\pm 53)$ km in temperature.

Both the shift in CTI (91 km) and the shift in temperature (273 km) were estimated independently with the same reasoning and suggest that birds are lagging 182 ± 53 km ($p < 0.001$) behind climate warming (99.9% CI of the difference $273 - 91$: 3.60–362).

4. DISCUSSION

Individual species are not randomly distributed in space. Instead, species distributions are limited by many factors (Clarke & Gaston 2006) among which climate, and

especially temperature, plays a major role (Thuiller *et al.* 2004): some species are found mainly in cold climates and others mainly in hot climates. We thus estimated an STI to account for this variation in species distribution among bird species. Obviously, the STI may suffer from many biases. In particular, our knowledge of the exact species' distribution is limited and highly dependent on data availability. However, we did not aim to estimate the actual temperature STI of a given species, but rather to order species along a gradient of low to high temperature dwellers. Interestingly, this ordering should not be influenced by biases affecting each species-specific STI and is robust to the data source used (e.g. French distribution versus European distribution, the widest reliable atlas available).

Of course, a species' distributions are not fixed, and even in the short term, ongoing climate changes have modified species' distributions at their margins (Thomas *et al.* 2001) so that a given species' STI is also likely to change from year to year. However, these species-specific changes should be very small compared with the range of variation of STI among species. Hence, the gradient of low to high temperature dwelling species, measured by fixed STI calculated from historical climatic and distribution data, is unlikely to have changed substantially over the last 20 years.

We further calculated the average STI of a given species assemblage recorded at each FBBS point count, the CTI, and the temporal trend of CTI over the last 18 years on more than 1500 sampled plots spread over France (figure 2). We found that the temporal trend of CTI was highly positive, suggesting that species with high STI have consistently replaced species with low STI during the last two decades.

As expected, CTI varies spatially and is strongly decreasing from south to north. This south–north gradient in CTI provides an estimate of the rate of change in community composition from south to north, which is influenced by temperature but also by other climate components, interactions with other species, habitat structure and dynamics, and dispersal limitation. We thus used this south–north gradient in CTI to calibrate the observed temporal change in CTI. In doing so, we found a 91 km northward shift in community composition. Our estimation is remarkably robust to the use of presence–absence rather than abundance data and was also similar using atlas data instead of FBBS data. In other words, we estimated that the change in species composition is occurring at a rate of 5.35 ± 0.64 km yr^{-1} (91 km divided by 17-year intervals). This change is produced by the average change in species distribution over their entire range.

Interestingly, this change is occurring up to eight times faster than the average change in species range edges previously estimated (e.g. 0.61 km yr^{-1} ; Parmesan & Yohe 2003, but see Hickling *et al.* 2006). We believe our estimate is higher because our approach integrates gradual changes within the core of species' distributions instead of relying on changes of species' range edges. Therefore, our results suggest that species are experiencing greater changes within their range than at their margins. We thus anticipate that application of our proposed framework to other available datasets will confirm that changes in species composition induced by climate warming are more rapid than suggested by previous studies.

During the study period, temperature in France increased at a very fast rate ($0.068^{\circ}\text{C yr}^{-1}$). This temperature increase is equivalent to a northward shift of 273 km in temperature over the last 18 years, whereas during the same period, the observed bird response is equivalent to a 91 km northward shift in community composition. Thus, despite their strong responses to temperature increase, birds are in fact lagging behind climate warming. This lag may be caused by strong climate warming acceleration in recent years that birds are just currently tracking. However, there is no sign that the rate of change in bird composition is accelerating: changes in bird composition is, in contrary, consistently linear (figure 2). We suggest that this result reflects that bird composition is most likely changing at its maximal possible rate, which is insufficient to catch up with the accumulated delay. This discrepancy may have profound consequences on the ability of species to cope with climate change in the long run.

Obviously, some species may have adapted by moving to higher elevations (Wilson *et al.* 2007; Lenoir *et al.* 2008; Sekercioglu *et al.* 2008), and studying the altitudinal shift in community composition would be very interesting with other datasets. The observed lag in change of species composition could also be due to local species adaptation to higher temperature. Yet, although genetic shifts could modulate local effects of climate change (Rehfeldt *et al.* 2002), there is little evidence that they will mitigate negative effects at the species level (Parmesan 2006). Moreover, only few studies indicate evolutionary responses of particular species to climate change (De Jong & Brakefield 1998) so that the generality of evolutionary response remains unknown (Parmesan & Yohe 2003) and unlikely to occur fast enough for many species anyway (Bradshaw & Holzapfel 2007). Thus, although we were not able to disentangle the real lag from possible local adaptation of birds to temperature increase, we believe that these adaptations (if any) were only responsible for a small amount of the apparent lag calculated in this study.

STI is the most objective and easy metric to calculate with most large-scale monitoring data. Moreover, an increase in the average STI of a given local assemblage (i.e. the CTI) should most often mirror the balance between low- and high-temperature dwelling species, and can be calculated either with abundance or presence-absence data. Yet, STI is only one among many facets of the species climatic envelope. In particular, it gives no information about the breadth of a species' thermal range with respect to temperature, which was shown to be a good predictor of bird populations' resilience to extreme high temperature (Jiguet *et al.* 2006). Therefore, although CTI should be a valuable indicator in many situations, other facet of the temperature niche could be used to monitor other community-level metrics than CTI, depending on the data available and the question being asked.

Although the exact numerical results of the lag found using our approach is not flawless, we think that this approach will be highly meaningful for comparative studies. Indeed, more crucial than any absolute lag in bird communities behind climate warming is the highly probable disruption of synchronization induced by this lag in species interactions (Harrington *et al.* 1999; Lenoir *et al.* 2008). Species differ in their physiological tolerances, life-history strategies, probabilities of population extinction

and colonization, and dispersal abilities. These individualistic traits probably induce high variability in strength of climate response across species, even among those subjected to similar climatic changes (Parmesan 2006).

For instance, it is likely that generalist and specialist species are not similarly lagging behind climate warming due to the difference in their response to land-use changes (Warren *et al.* 2001; Devictor *et al.* 2008). Assessing how this lag is distributed among groups of species of particular concern (e.g. specialist versus generalist, threatened versus unthreatened and good versus poor dispersers), or assessing whether the lag is similar between different kinds of sites (protected versus non-protected and fragmented versus non-fragmented) should be highly informative and valuable to drive more specific conservation options in the context of global changes.

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