Local extinction synchronizes population dynamics in spatial networks

Stephen F. Matter^{1,*} and Jens Roland²

¹Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45230, USA

²Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Spatial population theory predicts that synchrony in the dynamics of local populations should decrease as dispersal among populations decreases. Thus, it would be expected that the extinction of local populations and the attendant loss of immigrants to surrounding populations would reduce synchrony. We tested this hypothesis through a large-scale experiment, simulation of the experimental system and general models. Experimental removal of two adjacent subpopulations of the Rocky Mountain Apollo butterfly, *Parnassius smintheus* within a network consisting of 15 other local populations resulted in a decrease in immigration to surrounding populations that was proportional to their connectivity to the removal populations. These populations also showed a significant increase in synchrony during population removal. The spatial extent of the synchrony showed good agreement with the predicted loss of immigrants owing to the removals. Simulation of the *Parnassius* system showed a similar short-term result and also indicated that permanent loss of populations produces structural changes increasing synchrony. General models indicate that an increase in synchrony following extinction occurs when populations undergoing extinction have different carrying capacities than surrounding populations. The result is not owing to biased migration *per se*, but rather is because of the number of immigrants relative to the carrying capacity. Synchrony following extinction should be most common for patchy populations, but can occur in any situation where carrying capacities differ. Overall, our results indicate that local extinction can create a positive feedback for extinction risk, increasing the probability of extinction for population networks by synchronizing their dynamics.

Keywords: metapopulation; Moran effect; immigration; metapopulation level Allee effect

1. INTRODUCTION

Many species show synchronous population dynamics (Ranta *et al.* 1995). Synchrony in the dynamics of a single species is generally thought to arise through two main mechanisms (Liebhold *et al.* 2004). First, dispersal among populations can unite their dynamics (Hanski & Woiwood 1993). Second, exogenous forcing either by density-dependent or density-independent factors can synchronize dynamics. Moran (1953) proposed that populations with similar, linear density-dependent structures would become synchronized by spatially correlated, density-independent factors, in particular weather. This phenomena later was dubbed the ‘Moran effect’ (Royama 1992). Both of these processes produce synchrony in population dynamics that is spatially correlated with the extent related to the spatial scale of each (Sutcliffe *et al.* 1996; Lande *et al.* 1999).

Synchrony in the dynamics of local populations reduces the persistence of population networks (Harrison & Quinn 1989; Allen *et al.* 1993; Heino *et al.* 1997; Palmqvist & Lundberg 1998; Matter 2001). Most metapopulation models assume that the extinction risk of local populations is uncorrelated (Hanski 1999). If local populations are synchronous, extinction risk is correlated. For instance, synchronous populations could be simultaneously low at the time of a stochastic event. Such correlation in extinction risk reduces the probability of persistence for networks of populations because all local

populations may experience extinction simultaneously, or if only some populations experience extinction, there will be fewer populations remaining to recolonize those patches.

Spatial population theory predicts that populations linked by frequent dispersal should be more synchronous than those exchanging fewer migrants (Allen *et al.* 1993; Hanski & Woiwood 1993; Sutcliffe *et al.* 1996; Heino *et al.* 1997; Palmqvist & Lundberg 1998). Thus, one prediction would be that the extinction of a local population decreases synchrony owing to a reduction in dispersal to remaining populations. Alternatively, the simultaneous loss of immigrants resulting from local extinction may synchronize populations in a manner similar to the Moran effect. Here, we investigate the effects of local population extinction on synchrony using experimental and modelling approaches.

2. MATERIAL AND METHODS

(a) *Experimental system*

Our model species, the Rocky Mountain Apollo butterfly, *Parnassius smintheus* Doubleday, is a common butterfly in the Rocky Mountains. At our site they are found in alpine meadows where their host plants, *Sedum lanceolatum* L. and *Rhodiola integrifolia* Raf, occur (Roslin *et al.* 2008). Adults feed within the meadows on nectar from several plant species with yellow flowers (Matter *et al.* 2009). There is one generation per year. Females lay eggs singly near, but not

* Author for correspondence (mattersf@uc.edu).

on, host plants (Fownes & Roland 2002). First instar larvae overwinter within the egg and emerge shortly after snowmelt. Adults emerge in mid-July at our site.

Experimental work was conducted in a series of 17 populations along Jumpingpound Ridge, Alberta, Canada (figure 1). In 1995 and 1996 and from 2001 to 2007, individual mark–recapture methods were used (Roland *et al.* 2000; Matter *et al.* 2004). We censused each population four to six times per year during sunny, warm conditions. Butterflies were netted and marked on the hind wings with a unique 3-letter code using permanent ink. In most years we made more than 2000 captures of 1000 individuals, averaging about two captures per individual. From 1997 to 2000, butterfly abundances were estimated from standardized transect counts (Pollard & Yates 1993).

To simulate local extinction from a spatial population perspective, from 2001 through 2007 all adult butterflies were removed from meadows P and Q every 1–3 days, weather permitting. Abundance of *P. smintheus* for each population was estimated each year from 1995 through 2007. In most cases, population sizes were estimated using Craig's method (Craig 1953), which produces highly accurate results (Matter & Roland 2004). Transect counts were converted to a common scale based on the known relationship between the estimates (Matter & Roland 2004). The maximum estimate of abundance each year among the repeated estimates each summer was used as our estimate of population size that year. The number of immigrants to each population was simply tallied. This method underestimates the total number of migrants, but is unbiased in the statistical model after correcting for abundance and sampling effort.

To examine the effect of population removal on immigration, we compared a statistical model including populations P and Q to a model where the effects of these populations were excluded, simulating their extinction. The model included connectivity and the methodological variable of the number of times a meadow was censused each year, which increases with the observed number of immigrants. Connectivity was calculated as

$$S_j = A_j^{0.93} \sum_{k, k \neq j}^n (e^{-4.27d_{fjk} - 2.28d_{mjk}} 0.05A_k^{-0.42})N_k,$$

where S_j , the connectivity of population j , is a function of its area (A_j), the distance between it and source population k comprised of forest (d_{fjk}) and open habitat (d_{mjk}), the area of the source population (A_k) and its abundance (N_k). Parameters were estimated using the Virtual Migration Model and data from 1995 and 1996 (Hanski *et al.* 2000; Matter *et al.* 2004). The expectation is that if population removals affect immigration, connectivity not including populations P and Q should show a better fit to the number of immigrants than would models including P and Q. As the model not including P and Q will always predict fewer immigrants than the model assuming that there are populations in these meadows, a better fit by the extinction model also indicates a reduction in immigration that is proportional to the reduction in connectivity.

Meadow characteristics for connectivity were determined from 1:40 000 scale aerial photos taken in 1993. We estimated the distance (km) between centroids of butterfly capture in each meadow. We separated that total distance into portions through forest and meadow along the ridge

Figure 1. Populations of *P. smintheus* along Jumpingpound Ridge, Kananaskis Country, Alberta, Canada (50°57' N, 114°54' W). The 17 meadows and corresponding local populations are outlined. Meadows consist of grasses, mountain avens and wildflowers, including the butterflies' host plants lance-leaved stonecrop (*Sedum lanceolatum*) and ledge stonecrop (*Rhodiola integrifolia*). Meadows are bordered by forest consisting of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Forest is a strong barrier to butterfly dispersal (Matter *et al.* 2004). Bars between meadows indicate thin or incomplete tree-line. Meadow Z is separated from a large open area (Cox Hill), which periodically contains butterflies, but at a very low density. All butterflies were removed from P and Q during 2001–2007. Scale bar, 1 km.

top, as these butterflies rarely cross valleys (Roland *et al.* 2000). To avoid bias owing to butterflies not being marked in meadows I, J and K in 2001 and 2002, we restricted the analysis of immigration to 2003–2007. The number of immigrants consists of count data, thus we used generalized linear models assuming a Poisson error distribution and a log-link function. We corrected for over-dispersion by using a quasi-Poisson distribution for significance tests (Maindonald & Braun 2007). Because there was the same number of parameters for each model, we compared models based on the difference in deviance explained and Mallows' C_p statistic (Maindonald & Braun 2007).

Before examining changes in synchrony, we first assessed its potential spatial extent. Based on the connectivity metric above, we calculated the mean (2001–2007) reduction in connectivity resulting from the removals. These data show that effects should extend east to meadow S (a mean of 75.9% reduction in connectivity) and northwest to L (a mean 2.7% reduction). Populations to the north are virtually unaffected. Meadow H showed a mean reduction

Figure 2. Effects of experimental extinction on immigration to surrounding populations on Jumpingpound Ridge. (a) The relationship assuming that populations in P and Q were extant. (b) The relationship assuming extinction in P and Q. Populations most affected by the removals (L, M, N, O, R and S) are indicated by a black circle, other populations by a white circle. A Poisson regression model showed that a connectivity metric assuming extinction in meadows P and Q better fitted the observed number of immigrants than did a model including the effects of P and Q. The results indicate that population removals reduced immigration to surrounding populations in proportion to their connectivity to the removals. Analysis included the methodological factor, the number of times a population was censused.

in connectivity of 0.08 per cent resulting from the removals. Hence, we can use this population and the more distant F, G, g, Y and Z as controls, although as a group they are less isolated, share more migrants, and thus should be inherently more synchronous.

To assess the effects of removals on synchrony we calculated the pair-wise correlation (r) in abundance for populations affected by the removals (L, M, N, O, R, S) prior to (1995–2000) and during population removal (2001–2007). We compared z -transformed correlation coefficients using a paired t -test to determine if synchrony was affected by population removals (Zar 1999). To control for synchrony induced by other factors we also compared synchrony before and after extinction for the six control populations. We assessed the spatial extent of synchrony from 2001 to 2007 by calculating synchrony after incorporating each successively distant population from the removal meadows P and Q (e.g. R and O, then R, O, N, etc.); we also examined spatial extent by comparing the total synchrony of each successively distant population before and

Figure 3. Results of experimental extinction for populations on Jumpingpound Ridge. Populations near the local extinctions (L, M, N, O, R and S) lost immigrants owing to the removal of populations P and Q. Immigration to distant populations (F, G, g, H, Y, Z) was unaffected by the removals. We used paired t -tests to compare synchrony prior to and during extinction, after z -transformation. Significant differences (two-tailed $p < 0.05$) are indicated by double-asterisks (**). Means are shown ± 1 s.e. Synchrony across the entire ridge increased during the study owing to a population crash in 2003, and locally owing to the removals. Black bar, before removal; grey bar, during removal.

during removals. We assessed temporal effects in a similar manner. Here the populations found from the spatial extent (L, M, N, O, R and S) were examined during the first 3 years, 4 years, etc. over the 7-year duration of the experiment.

(b) Simulation modelling

To determine if our experimental results were robust, we simulated our experimental system. To do so we simulated 17 discrete logistic populations of the form

$$N_{t+1} = N_t e^{r(1-N_t/K)}.$$

The carrying capacity (K) for each was set by the mean abundance observed from 1995 to 2000. As there is a yearly correlation in growth among populations (Roland & Matter 2007), the intrinsic rate of increase (r) was first set by a yearly rate randomly drawn from a normal distribution set by the observed mean and s.d. (0.09 ± 0.94), where $r = \ln(N_{t+1} + 0.1/N_t + 0.1)$. This growth rate was then allowed to vary among populations within years based on the mean observed s.d. in growth among populations within years (± 1.01). Dispersal occurred after reproduction and was modelled according to the connectivity metric above using the observed habitat areas and interpatch distances.

Populations were initialized at a value between 1 and 115 per cent of their carrying capacity. We ran 1000 simulations for 103 generations, with extinction of populations P and Q occurring in generation 100. We compared the mean of the correlation coefficients for all pairs of populations affected by the loss of immigrants (L, M, N, O, R, S) before and after extinction. Similarly, we compared the six control populations (F, g, G, H, Y, Z) unaffected by the removals. We used paired t -tests to compare the mean correlation in the abundance of populations for the three generations before and after extinction. To examine the temporal extent

Figure 4. Spatial and temporal extent of synchrony in the Jumpingpound experimental system. (a) Mean correlation before and during population removal between the two populations closest to the removals (O, R) followed by the mean correlation among three closest (O, R, N), four closest, etc. Means are shown ± 1 s.e. Because only two populations were compared, there is no error for the comparison of O and R. (b) Mean correlation in abundance considering all populations. Populations are ordered with increasing distance from the removal populations. Black bar, before removal; grey bar, during removal. (c) Temporal extent of synchrony. The mean correlation for populations L, M, N, O, R and S during the first 3, 4 years, etc. following extinction is shown.

of synchrony following extinction, we ran the model for 200 generations and compared synchrony of affected and control populations in the three generations prior to extinction to the final three generations.

(c) General model

To extend our investigation of the effects of extinction under a similar but broader set of conditions, we used a system of eight discrete, logistic populations. All populations had a starting abundance between 0 and 1.15 times the carrying

capacity and an independent, stochastic component up to ± 15 per cent of the carrying capacity each generation. For all runs, populations were simulated for 103 generations. At generation 100, two populations were set and maintained at an abundance of zero to simulate their extinction. We ran 1000 simulations for each parameter combination and compared the mean synchrony of the remaining six populations before and after extinction. We used paired *t*-tests (two-tailed probability) to compare the mean correlation in abundance among all pairs of populations for the three generations

Figure 5. Simulation of the 17 local populations in the Jumpingpound system. Synchrony before and during local extinction of P and Q were compared for populations near the local extinctions and more distant control populations unaffected by the removals. Models were run for 103 generations and we used paired *t*-tests to compare synchrony for the three generations prior to and after the extinctions that occurred in generation 100. Means of 1000 simulations are shown ± 1 s.e. Significant differences (two-tailed $p < 0.05$) are indicated by double asterisks (**). Black bar, before removal; grey bar, during removal.

before and after extinction, i.e. one comparison for each simulation run.

We first investigated factors known to affect synchrony (Ranta *et al.* 2006), but for which effects on synchrony following local population extinction were unknown. Models were run for emigration rates of 0.05, 0.15, 0.25 and 0.50, simulating varying amounts of dispersal among populations. Population growth rates of 1.1, 2.1, 3.1 and 4.1 were used to simulate a range of dynamics (May 1974). For initial models, all populations had a carrying capacity of 100 and dispersal among populations was global (i.e. all populations were equally accessible).

Following these simulations, we investigated factors present in the *Parnassius* system possibly accounting for synchrony following extinction (see §3). We introduced spatially structured dispersal by altering the dispersal distance among populations using a negative exponential dispersal function as in the connectivity metric above. Populations were arranged linearly, similar to our ridge system. Each population was one unit distant from the next and extinction occurred in the middle two populations. The parameter α (multiplied by interpatch distance in the connectivity metric), which is the inverse of mean dispersal distance, was set at 1, 0.25 or 0.001 (global dispersal).

To examine whether biased dispersal between populations undergoing extinction and the surrounding populations may alone produce synchrony, we ran simulations where populations undergoing extinction had double the emigration rate of surrounding populations. These simulations were run at the levels used above (0.05, 0.15, 0.25), except that cases where emigration equalled 0.50 were not investigated. We also examined whether differences in carrying capacity between the extinction populations and surrounding populations affect synchrony following extinction. Here, populations undergoing extinction had a carrying capacity

of 250 and surrounding populations a carrying capacity of 25, and *vice versa*. Finally, we jointly examined biased dispersal and heterogeneous carrying capacities.

3. RESULTS

(a) Experimental

We removed 4380 butterflies from populations P and Q over the 7 years. The number of immigrants to surrounding populations decreased in proportion to their connectivity to the removals (figure 2). The statistical model including the extinction of P and Q was a better predictor of immigration than was the model not including their extinction (extinction model: deviance explained = 111.3, $F_{1,79} = 12.6$, $p < 0.001$, Mallow's $C_p = 647.9$ (smaller is better); no extinction: deviance explained = 98.9, $F_{1,79} = 10.9$, $p = 0.001$, Mallow's $C_p = 661.8$). These results indicate that the removals had their intended effect, and reduced immigration to surrounding populations in proportion to their connectivity to the removal populations.

Synchrony among populations affected by the removals (those near the removals) was significantly higher during the removals than before the removals (paired $t = -2.73$, d.f. = 13, two-tailed $p = 0.02$). More distant populations showed no difference in synchrony during the population removal versus prior (paired $t = -1.13$, d.f. = 13, two-tailed $p = 0.28$; figure 3). We note that overall synchrony increased across the entire ridge during the study. This increase was probably due to a Moran effect. Over-wintering survival from 2002 to 2003 was low, resulting in low adult abundances for all populations in summer 2003. Despite this perturbation, the spatial extent of synchrony showed a good correspondence to the estimated spatial extent of the removal for immigration, indicating that the removals induced greater synchrony (figure 4a). Synchrony among the populations near the removals decreased over time, but was still high throughout the experiment (figure 4c).

(b) Simulation

Simulation of the *Parnassius* system on Jumpingpound Ridge showed similar results. Removal of populations in meadows P and Q resulted in increased synchrony, consistent with a Moran-like effect. Synchrony among populations close to removals increased (paired $t = -21.78$, d.f. = 999, two-tailed $p < 0.01$), while the synchrony among distant control populations decreased slightly, but significantly (paired $t = 4.92$, d.f. = 999, two-tailed $p < 0.01$; figure 5). Simulation of the system for 100 generations following extinction and comparing the three generations prior to extinction to the final three generations showed lasting effects for populations near the extinctions (paired $t = -41.64$, d.f. = 999, two-tailed $p < 0.01$), but not for distant populations (paired $t = 1.45$, d.f. = 999, two-tailed $p = 0.15$). These results indicate that the extinctions also produced fundamental changes in spatial structure that increased synchrony. These changes largely involved much higher synchronization of N, R and S with O when populations P and Q were extinct than when they were extant, e.g. for N–O, $r = -0.33$ prior to extinction and $r = 0.87$ after extinction.

Figure 6. General model of the effects of local population extinction synchrony. For these models all eight populations had an equal carrying capacity ($K = 100$) and dispersal was spatially structured. Models were run under the emigration rates (em) and population growth rates (r) indicated. We used paired t -tests to compare synchrony for the three generations prior to and after the extinctions that occurred in generation 100. Significant differences (two-tailed $p < 0.05$) are indicated by double asterisks (**). Means ($n = 1000$) are shown ± 1 s.e. Black bar, before extinction; grey bar, after extinction.

(c) General model

Simulation of the extinction of two populations within a system of eight populations showed a general decrease in synchrony following extinction where all populations were of the same size and dispersal was global. Results of these simulations generally agree with previous studies of the effects of dispersal and growth rates on synchrony (e.g. Heino *et al.* 1997). Similarly, spatially structured dispersal affected synchrony, but did not result in an increase in the amount of synchrony following local extinction. Here, any significant changes resulted in decreased synchrony following extinction (figure 6).

Spatially structured models where the emigration rates from populations undergoing extinction were double that of surrounding populations showed that biased dispersal alone is able to synchronize populations following extinction, but only under very limited conditions. We found a significant increase in synchrony following extinction under a growth rate of 4.1 and emigration rates of 0.10 for populations undergoing extinction and 0.05 for surrounding populations. We note that populations were largely asynchronous both before and after extinction. These simulations also resulted in decreased synchrony following extinction. All emigration rates under growth rates of 2.1, and for emigration rates of 0.25 (surrounding populations) under growth rates of 3.1 and 4.1, resulted in significant decreases in synchrony following extinction.

When carrying capacities differed between populations undergoing extinction and surrounding populations, we found very different results. When populations undergoing extinction had carrying capacities of 250 versus 25 in surrounding populations, the majority of cases resulted in increased synchrony following extinction (figure 7), but there were also cases where synchrony was reduced or no difference was seen. When carrying capacities were reversed and those undergoing extinction were 25 and surrounding populations 250, we found increased synchrony following extinction, where $r = 3.1$

and $em = 0.15$; and $r = 4.1$ and $em = 0.05$; however, both cases represented decreased asynchrony rather than synchronous populations.

For cases where both emigration and carrying capacity were greater for populations undergoing extinction increases in synchrony following extinction were largely magnified for population growth rates of 1.1 and 2.1 versus similar runs without biased dispersal (figure 7). For higher growth rates, biased dispersal produced varied results, producing both increases and decreases in synchrony following extinction. Finally, we re-ran this simulation for global dispersal, e.g. $\alpha = 0.001$. Qualitatively, the results were the same for growth rates of 1.1 and 2.1, but where $r = 3.1$ and $em = 0.15$ and $r = 4.1$ and $em = 0.25$ cases where synchrony had increased changed to decreases following extinction indicating some effects of spatially structured dispersal.

4. DISCUSSION

Our results show that local population extinction can synchronize the dynamics of spatially structured populations. In the Jumpingpound system this occurs through two mechanisms. First, the loss of immigrants to surrounding populations can induce a Moran-like effect. Reduction of immigration resulting from extinction simultaneously depresses abundance in surrounding populations, producing more synchronous dynamics. Second, our simulation of the Jumpingpound system indicates that local population extinction can produce fundamental changes in the structure of spatial populations resulting in increased synchrony. Here, extinction causes populations that were previously maintained asynchronously to become synchronous. This effect is because of large intervening populations (e.g. P and Q) collecting immigrants from smaller surrounding populations and a destabilizing effect of immigrants from the large populations for smaller populations when the large populations are extant. When large populations

Figure 7. General models of the effects of local population extinction synchrony. For these models dispersal was spatially structured and run under the emigration rates (em) and population growth rates (r) indicated. Both panels show cases where the populations undergoing extinction had a carrying capacity of 250 while surrounding populations had a carrying capacity of 25. (a) Cases where emigration rates were equal for all populations; (b) runs where emigration rates from populations undergoing extinction were double that of surrounding populations (level indicated). We used paired t -tests to compare synchrony for the three generations prior to and after the extinctions that occurred in generation 100. Significant differences (two-tailed $p < 0.05$) are indicated by double asterisks (**). Means ($n = 1000$) are shown ± 1 s.e. Black bar, before extinction; grey bar, after extinction.

experience extinction, migration among the smaller populations can act to synchronize them with the largest population becoming the driver. Both effects are evident in our experimental results. Populations near the removals were asynchronous prior to the removals and became highly synchronous during the removals, demonstrating structural changes. The strength of synchrony during the removals decreased extending from the removal populations, illustrating the effect of the loss of immigrants.

It is important to note that we have not precisely identified conditions under which local extinction will produce increased synchrony; we have simply shown where it is possible. In many cases and with relatively small changes, conditions can flip from those resulting in increased synchrony following extinction to those resulting in decreased synchrony. Furthermore, different runs for

most sets of parameters could show either increased or decreased synchrony following extinction. Thus, it is not a foregone conclusion that local extinction will increase synchrony among remaining populations. Our modelling results show that it is necessary that populations differ in carrying capacity for synchrony to increase following local extinction. This result echoes those seen for the effects of population heterogeneity on synchrony itself (Matter 2001; Engen *et al.* 2002; Hugueny 2006). In general, these studies show that among-population variation in carrying capacity or density-dependence tends to reduce synchrony, but can also produce non-intuitive results. As most natural populations in spatial networks differ in carrying capacity, these conditions should not be restrictive and need to be accounted for in the studies of synchrony (Hugueny 2006), extinction and of spatial population dynamics in general.

Our results indicate that patchy populations (i.e. those with high amounts of dispersal among local populations) are most likely to exhibit an increase in synchrony following extinction. Thus, patchy populations should have an increased risk of global extinction following local extinction. However, metapopulations, with lower rates of inter-population dispersal, are not immune to this effect. Several factors may act to ameliorate the effects for metapopulations. First, because synchrony in metapopulations may be low to start, any increase owing to extinction may not result in highly synchronous dynamics. Second, synchrony following extinction is greatest when large populations going extinct are surrounded by smaller populations. As large populations generally have a lower risk of extinction than do smaller populations (Richter-Dyn & Goel 1972; Hanski 1994), this situation may be less common in natural systems, and is more likely to occur where extinction results from factors such as habitat destruction.

When population extinction occurs on a relatively small spatial scale, there can be positive feedback for the persistence of networks of populations. Not only will potential colonists from the extinct populations be lost, nearby populations can become synchronized. Thus, extinction can increase the likelihood of further or global extinction, particularly where stochastic events play an important role, such as the highly capricious alpine environment or where metapopulation-level Allee effects occur (Amarasekare 1998). To date, our system has not experienced any increase in extinction resulting from either the removals or the increased synchrony. Despite no increased extinction in our system, studies that do not account for this positive feedback in extinction risk probably overestimate persistence, particularly in stochastic environments or where extinction results in structural changes increasing synchrony.

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