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Displacement and replacement in real time: *Polistes dominula's* impact on *P. fuscatus* in the northeastern U.S.

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Abstract Two major challenges in studying the impacts of exotic invasive species on native species are identifying mechanisms of displacement and replacement and the lack of long-term population studies in these systems. A solution for the first is to study invasive and native congeners that occupy the same niche. A solution for the second is to study many populations for one year instead of one population for many years. We studied the invasion biology of the invasive European paper wasp *Polistes dominula* and its native congener the Northern paper wasp *P. fuscatus*, two species which compete for similar resources. We tracked the demography of the two wasps at sites in the northeastern United States. We found that the survival of *P. dominula* to the reproductive period in August was three times that of *P. fuscatus*, across all sites. The reproductive output of *P. fuscatus* declined in direct proportion to the percentage of *P. dominula* nests at the site. *P. fuscatus* nests at uninvaded sites had three times the nest cells of those at the most invaded sites. These findings suggest a positive feedback cycle in the establishment of *P. dominula*, in which the invasive wasp drives population declines in the native that in turn allow *P. dominula* to further establish. This system provides an example of a possible extinction vortex caused by competitive exclusion of a species by its invasive congener.

Keywords Polistes · Invasion biology · Competitive exclusion · Local extinction · Displacement

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Introduction

Biological invasions are a leading contributor to species loss (Vitousek et al. 1996; Chapin et al. 2000). Invasive species are implicated as a cause of 54% of the extinctions on the IUCN Red List for which data are available (Clavero and García-Berthou 2005). Invasive species are commonly defined as species introduced outside their native ranges that subsequently establish, spread, and have negative environmental impacts (Lodge et al. 2006). They can cause local extinctions through a variety of mechanisms, including predation, competition, disease, and habitat alteration (Mack et al. 2000). However, it can be difficult to identify precise causal links between the presence of an invasive species and population

declines of native species within its range, leading some to question whether the role of biological invasions in species loss has been overstated (Gurevitch and Padilla 2004; Towns et al. 2006).

Conservation biologists are deeply invested in the question of how extinctions occur, employing theoretical and observational approaches (Benton 2003). Longitudinal studies of declining populations are invaluable for understanding the process of local extinction (Fagan and Holmes 2006); however, long-term population studies are scarce (Matthies et al. 2004; Ojanen et al. 2013). An alternate approach is a cross-sectional study, substituting space for time across sites that have been invaded more or less recently, as proxies for different timepoints in the invasion (Donlan and Wilcox 2008). Even so, it is not always clear whether native species are being displaced from their original niches, directly attacked, competitively excluded from a shared niche, or affected by habitat alteration by the invader.

Invasive social insects count among the most ubiquitous and destructive species (Lowe et al. 2000; Rust and Su 2012). A single fertilized female can produce hundreds of offspring, which means that one gyne can constitute a viable propagule; further, social insects are notable for their cooperative behavior and flexible social structures (Moller 1996; Suarez et al. 2008). Indeed, introduced social insects are more likely to become invasive than their solitary congeners (Beggs et al. 2011). Invasive social insects are not only an important phenomenon in themselves; they also provide a unique opportunity to study the processes by which invasive species cause local extinctions. Social insects are cosmopolitan in their distribution, which means that nearly anywhere they are introduced, there are closely related species occupying a similar niche. Therefore it is much easier to link native species' decline to direct or indirect competition with the invasive congener.

The European paper wasp *Polistes dominula*, and its native congener the Northern paper wasp *P. fuscatus* are an excellent system in which to study the process of local extinction by an invasive species. *P. dominula* was first noticed in North America in Massachusetts, U.S., in 1978 (Eickwort 1978); by 1998, they had been found in the Midwest states and California (Liebert et al. 2006). It is highly unlikely the wasp dispersed naturally in such a short period, and indeed the genetic evidence confirms multiple

introductions, which indicates that these observations across the United States were outbreaks of already established introduced populations (Johnson and Starks 2004; Liebert et al. 2006).

In the Northeast and Midwest, *P. dominula* co-occurs with a native congener, *P. fuscatus*. Like most *Polistes*, *P. fuscatus* is a nectar feeder as an adult and carnivorous as a larva. Adults hunt and butcher Lepidoptera larvae to feed to their young. (See Brown et al. 2012 for a description of these foraging behaviors.) Nests are founded by fertilized females in May and defended vigorously against invaders; the worker brood emerges in July, and the reproductive brood in August. *P. dominula* and *P. fuscatus* have similar diets (Cervo et al. 2000), nest sites (reviewed in Liebert et al. 2006), and colony cycles (Gamboa et al. 2002, 2004). However, in nest box observations we see that *P. dominula* has higher foraging rates, higher reproductive output, and earlier worker production than *P. fuscatus* (Gamboa et al. 2002, 2004). When *P. dominula* nests are removed from nest boxes, *P. fuscatus* establishes nests in their place, which suggests that *P. dominula* competes with its native congener for nest sites (Miller et al. 2013; also see Downing 2012). At the same time, extensive videography and field surveys on nests of both species at sites where they coexist have revealed that direct agonistic encounters between wasps of the two species are extremely rare (Gamboa et al. 2002; Silagi et al. 2003). All of the evidence so far points toward competition as the mechanism of displacement of *P. fuscatus* by *P. dominula*. However, the demographies of *P. dominula* and *P. fuscatus* have only been compared at nest boxes set up specifically for the study of wasps, not at natural sites.

To study the impacts of competition on the invasive and native wasps in the northeastern United States, we observed naturally occurring nests of the two species across a broad spatial scale in Massachusetts and Maine, at sixteen sites with different proportions of *P. dominula* and *P. fuscatus*, ranging from *P. fuscatus* only to entirely occupied by *P. dominula*. Over the course of three time points in the colony cycle, we tracked nests at these sites and noted their persistence, development, and reproductive output. By observing nests of both species at sites with different proportions of each, we sought to understand how both species' demographies were impacted by the presence of the other.

Methods

Observations

In 2016 we surveyed 16 sites in Massachusetts and southern Maine (Table S1), including state parks, non-profit nature reserves, and private farms. Study sites were chosen based on where *Polistes* prefer to nest (Dew and Michener 1978): human-built structures with old wood for nest-building material and access to floral, faunal, and water sources. We surveyed the sites at three time points in the colony cycle: May 27–June 17, during the founding period, when nests are mostly established but workers have not yet emerged; July 25–August 1, during the worker period, when workers have emerged on nests as adults; and August 22–26, the reproductive period, when males and gynes have emerged on nests as adults. We searched the sites for nests by looking in the wasps' preferred nest sites: elevated sheltered sites with sunlight to warm them, which effectively meant the eaves of buildings in most cases. Each nest was photographed and the latitude and longitude noted so the site could be precisely checked; therefore, even nests that were wholly lost to predation could still be noted for their absence.

At each time point, the number of females, males, cells, eggs, larvae, and pupae were recorded for each nest in the early morning, when all wasps were present and dormant. We used these values to calculate maturity score on the nests. Maturity scores are calculated based on the time needed for eggs to develop into larvae and pupae (Strassmann and Orgren 1983; Starks 1998). A maturity score of 1 means that all cells in the nest are occupied by eggs, maturity scores lower than 1 indicate empty nest cells, and maturity scores higher than 1 indicate more development into larvae and pupae. Maturity score was calculated as follows:

$$M = \frac{1.00 Eggs + 2.28 Larvae + 3.90 Pupae}{Cells}$$

At the first time point, we measured distance to each nest's two nearest neighbors. At the second two time points, survival of nests found in the first survey was tracked. JAP also conducted thorough searches, with the same methodology as the initial survey described above, for any new nests established after the founding period at subsequent time points.

Statistics

We calculated survival of nests over the course of the season using binomial GLMs. We built models with the nest as the unit of observation and the nest's live or dead status as the dependent variable. The models were factorized with species, species of the nearest neighboring nest, distance to the nearest neighboring nest, number of foundresses on the nest, and proportion of the native species to the invasive at the site. All models contained site as a random effect. We competed them against the null using AICc (to account for small sample size) and used the best model to estimate survival from the founding period to the reproductive period.

For cell number and maturity score, we constructed a suite of GLMs with the same factors and random effect structure as the survival models, above. The best model for each time point was retained. We used a separate suite of models for each time point rather than pooling observations and using time point as a factor because we were tracking precisely the same group of nests over time, and observations would therefore be nonindependent between time points. We used the Poisson distribution for the cell number models, and the lognormal distribution for the maturity score models. All analyses were conducted in R v. 3.3.2 (R Core Team 2016).

Results

Summary statistics

We found 91 nests at 16 sites, consisting of 38 *Polistes dominula* nests and 53 *P. fuscatus* nests (Fig. 1). We found 74 of those nests in the founding period; the remaining 17 nests were built between the founding period survey and the worker period survey. Of the 17 new nests built in the worker period, 4 were *P. fuscatus* nests and 13 were *P. dominula* nests. By the time of the reproductive period survey, 40 of the 91 nests had died; 9 of the dead nests were *P. dominula* nests and 31 were *P. fuscatus* nests.

Survival

Persistence of nests from the founding period to the worker period was lower in *P. fuscatus* (mean: 0.746,
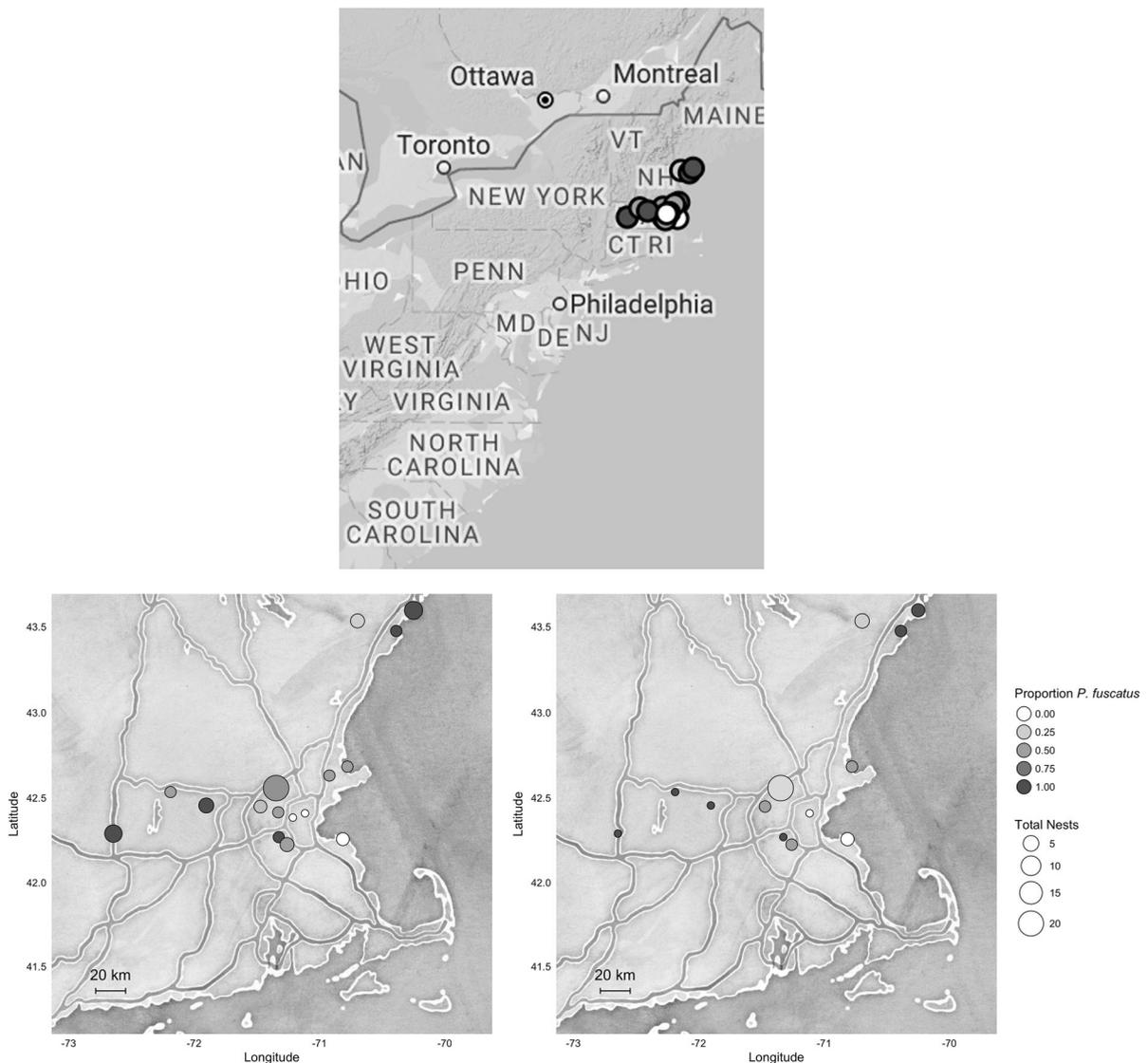
Fig. 1 A map of sixteen sites in Massachusetts and Maine which were surveyed three times in the summer of 2016 to track reproductive output and survival of native *P. fuscatus* and invasive *P. dominula* nests. The first map situates the study sites in North America. Below, the first survey in June is shown, then the final survey in August. The sites are coded by the ratio of *P. fuscatus* to *P. dominula* nests, and scaled by the number of living nests at the site

95% CI: {0.430, 1}) than in *P. dominula* (mean: 0.994, 95% CI: {0.843, 1}). Survival of nests from the founding period to the reproductive period was also lower in *P. fuscatus* (mean: 0.250, 95% CI: {0.116, 0.384}) than in *P. dominula* (mean: 0.731, 95% CI: {0.560, 0.901}). Survival in both species was unrelated to the presence of the other, nor was it related to the distance to, or species of, a nest's nearest neighbors ($\chi^2 = 0$, $df = 1$, $P = 1$). In both species, the probability a nest would survive to the worker period increased with foundress number (slope: 1.101, 95% CI of slope: {0.313, 2.147}) but the probability a nest would survive to the reproductive period did not (slope $= 0.632$, 95% CI of slope: {$- 0.214$, 1.478}).

Maturity score

Maturity score did not differ by species, nor did the presence of either species affect maturity score in the other, in the founding period or the worker period

(AICc lowest for the null model at both time points). In the reproductive period, *P. fuscatus* nests (mean: 0.437, 95% CI: {0.107, 0.346}) had higher maturity scores than *P. dominula* nests (mean: 0.226, 95% CI: {0.291, 0.583}); however, neither species was affected by the presence of the other ($t38 = -1.320$, $P = 0.429$). Foundress number and nearest neighbor distance had no effect on maturity score at any time point (AICc lowest for the null model at all time points).
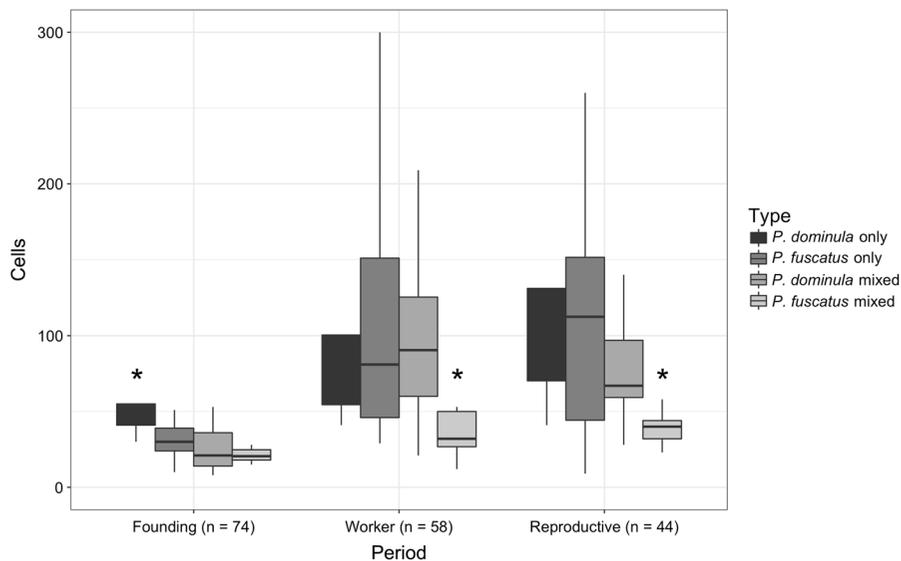
Cell number

In the founding period, cell number was lower in *P. fuscatus* (mean: 24.652, 95% CI: {18.704, 30.600}) than in *P. dominula* (mean: 36.527, 95% CI: {27.715, 45.340}); nest cells in each species were unaffected by the presence of the other ($\chi^2 = 2.838$, $df = 2$, $P = 0.242$). In the worker period, cell number was lower in *P. fuscatus* (mean: 94.8, 95% CI: {74.967, 120.013}) than in *P. dominula* (mean: 124.4, 95% CI: {115.035, 134.231}). Cell number in *P. fuscatus* nests decreased with increasing proportion of *P. dominula* at the site (slope: -2.383, $z58 = -6.569$, $P < 0.0001$;

Fig. 2). In the reproductive period, cell number continued to be lower in *P. fuscatus* (mean: 117.4, 95% CI: {92.875, 148.539}) than *P. dominula* (mean: 125.6, 95% CI: {116.160, 135.609}). Cell number in *P. fuscatus* nests decreased with increasing proportion of *P. dominula* at the site during this period as well (slope: -1.244, $z44 = -2.695$, $P < 0.01$; Fig. 3). Across the colony cycle, cell number was not affected by distance to nearest neighbors, nor whether these neighbors were the same species. In both species, cell number per foundress declined with foundress number at all three time points (95% CI of slope, founding: {-0.733, -0.641}, worker: {-0.972, -0.905}, reproductive: {-0.974, -0.900}).

Discussion

Our most striking result is the direct negative relationship between the proportion of *Polistes dominula* nests at a site and the reproductive output of *P. fuscatus* nests at that site. By the reproductive period of the colony cycle, *P. fuscatus* nests at sites without *P. dominula* had nearly three times as many cells on

Fig. 2 Cell number in nests of native and invasive wasps in Massachusetts and Maine. A box plot showing variation and change in cell number in native *P. fuscatus* and invasive *P. dominula* nests over the course of the summer of 2016. The nests were surveyed at three time points: the founding period, directly after worker emergence, and during the production of reproductives. This box plot compares cell number in nests of each species at sites where the other species was not present (only), and at sites where both species were present (mixed). Stars indicate which group is significantly different from the others at each time point ($P < 0.05$). After the first time point, nests that die are omitted from the graph, and new nests that are founded later in the season are added
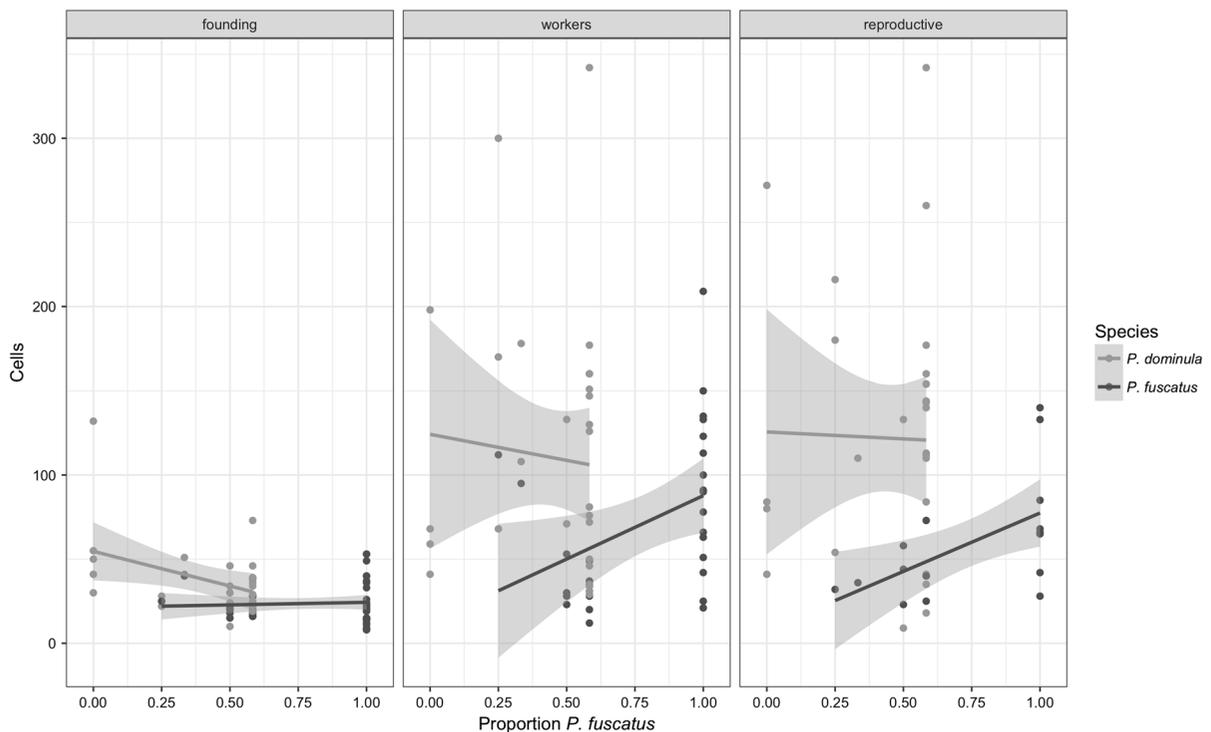
Fig. 3 Effect of species ratio on cell number in nests of native and invasive wasps. The graph shows the number of nest cells in native *P. fuscatus* and invasive *P. dominula* nests at 19 sites with different ratios of *P. fuscatus* to *P. dominula*. In *P. fuscatus* the number of cells per nest is proportional to the ratio of *P. fuscatus* present at the site, while in *P. dominula* cell number is unaffected by the species ratio

average as *P. fuscatus* nests at sites where 75% of the nests were founded by *P. dominula*. Considered alongside the survival to the reproductive period, which was three times higher in *P. dominula* than *P. fuscatus*, *P. fuscatus* is likely producing far fewer reproductives per colony cycle than *P. dominula*, especially at sites where it coexists with *P. dominula*. Our data indicate that *P. fuscatus* never truly thrives in settings where *P. dominula* is established, and the wide gap between the species' trajectories through the colony cycle, especially at mixed sites (Fig. 4), illustrates the disparity in the outcomes of the two species.

We propose that *P. fuscatus*'s loss of reproductive output in direct proportion to the presence of *P. dominula* results in a positive feedback cycle (Fig. 3). When *P. dominula* establishes at a site, *P. fuscatus* produces fewer reproductives, which opens more vacancies at the site for *P. dominula* to fill the following year. As the proportion of *P. dominula* increases, *P. fuscatus* is displaced further, in the classic pattern of the extinction vortex (Soulé et al.

1986; Fagan and Holmes 2006). With reference to Fig. 1, the process of replacement of *P. fuscatus* by *P. dominula* is apparent even over the course of one colony cycle, especially at our largest field site, which shifted from 58% native in June to 19% native in August. The observed increase in the proportion of *P. dominula* at experimental nest-boxes at the Oakland University Biological Preserve in Michigan from 1995 to 2011, from a single nest to 75% of all observed nests, is consistent with this finding (Miller et al. 2013). Because *P. dominula* has higher foraging rates and higher reproductive output than *P. fuscatus* (Gamboa et al. 2002, 2004), the ecological consequences of replacement of *P. fuscatus* by *P. dominula* may include higher predation pressure on Lepidoptera larvae at sites dominated by the invasive wasp. Also, *P. dominula*'s tolerance for more exposed nest sites means they can capitalize on sections of human structures that *P. fuscatus* would reject, which may increase overall *Polistes* abundance at sites where *P. dominula* predominates.
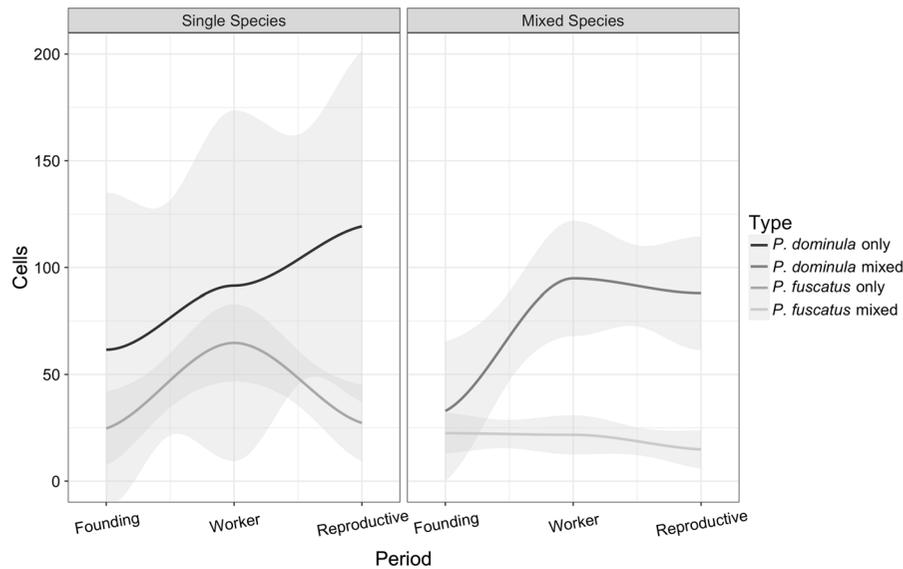
Fig. 4 Trajectories of effective reproductive output in native and invasive wasps. The graph shows trajectories of effective reproductive output in native *P. fuscatus* and invasive *P. dominula* paper wasp nests at sites where the other species is not present (single species) and sites where both species are present (mixed species). The gray ribbons behind the lines indicate 95% confidence intervals. Nests that died after the founding period are included as zeroes in the graph, because the reproductive output of a nest where all the adults have died is zero. The cell number at the reproductive time point is the most relevant to colony reproduction, as this is when males and fertile females are produced. The upward trajectories of the *P. dominula* curves indicate high fecundity and low mortality, resulting in a high reproductive output at the end of the colony cycle. The rise and fall in the curve for *P. fuscatus* at single-species sites indicates an increase in productivity mid-colony cycle, which then decreases because of high nest mortality in the reproductive period. The flat trajectory of *P. fuscatus* at single-species sites shows that high mortality effectively cancels out nest productivity at these sites

Our finding that survival is higher and per-foundress productivity lower on multiple-foundress nests is by no means novel (Gibo 1978; Tibbetts and Reeve 2003); multiple founding is a form of survivorship insurance, whereby nests are less likely to fail because of the high probability that at least one foundress will survive (Reeve 1991). However, our study highlights the relevance of this demographic variation to invasion biology. In Massachusetts and Maine, we observe no difference in the frequency of multiple founding between the two species, but the two species have different behavioral responses to climatic variation, so we would expect there to be different frequencies of multiple founding between the species in other regions (Sheehan et al. 2015; Pilowsky et al. submitted). Where *P. dominula* cooperatively breeds more frequently than the native wasp, its advantage in survival should be even greater.

There are caveats, however, both in terms of potential advantages to *P. fuscatus*, and the limitations of this study. First, it should be noted that the native wasp had significantly higher maturity scores in the reproductive period than the invasive wasp, which indicates that the native continues to produce reproductives later in the season than the invasive, perhaps an unsurprising finding given that the native wasp produces workers later than the invasive (Gamboa et al. 2004). Second, the native wasp is known to have greater thermal tolerances (Weiner et al. 2011) and higher overwintering survival (Gamboa et al. 2004) than the invasive, thus it is more likely to survive to the following spring. Third, the summer of 2016 saw a severe drought in the Northeast, which may have affected survival and productivity differentially in each species; the effects such stochastic climate events are an inherent disadvantage of cross-sectional studies across space conducted in 1 year. Fourth, we did not find any sites with low proportions of the invasive wasp—our least invaded site that was not native-only had a proportion of 42% invasive nests—which circumscribes our knowledge of the demography when *P. dominula* presence is limited. Finally, there were several sites we found in Massachusetts with high proportions of the invasive that we used for

collections for another study. We omitted these highly invaded sites from this study. As a consequence, the relative sample sizes of the native and the invasive wasp in this study actually overstate the proportion of native wasps we found in the region overall; therefore, our estimates here may be considered conservative.

While there were no apparent threshold effects in *P. fuscatus*'s response to the proportion of *P. dominula*, they may be present at densities of *P. dominula* we did not observe. There are possibly Allee effects for both species at low densities, as the sex determination system in Hymenoptera effectively sterilizes an increasing proportion of males as the genetic diversity in a population decreases, a phenomenon known as the diploid male extinction vortex (Liebert et al. 2004, 2005; Zayed and Packer 2005). It may be difficult for *P. dominula* to initially gain a foothold at a new site; the probability of successful establishment may be low, or it may require many simultaneous invaders to avoid the extinction vortex. However, we speculate that once a *P. dominula* population establishes in a site, a positive feedback cycle begins, and eventually *P. fuscatus* may be driven to such low proportions that it too is subject to the diploid male vortex. This process may in part account for the pattern of sudden outbreaks of the invasive wasp across the United States within the span of only 20 years (Liebert et al. 2006). We know from previous studies that *P. dominula* was introduced to the continent many times. If after many introductions a positive feedback cycle with native congeners took effect, the invasive population would have suddenly dramatically increased to the point that researchers took notice. This pattern of sudden simultaneous outbreaks of an invasive species across large geographic scales is not uncommon, and may be the result of a similar replacement process in other systems. However, longitudinal studies of sites invaded by *P. dominula* would be necessary to be confident in these speculations.

We were able to gain insight into the process of how invasive species can displace and replace their native congeners over the course of an invasion by looking across spatial scales rather than temporal scales. The range of proportions of native to invasive at our sites across Massachusetts and Maine were proxies for different time points of an invasion; after all, it is no accident that the proportion of *P. dominula* at our sites broadly decreased with distance from Boston, which

was almost certainly the port of entry from Europe for *P. dominula* in the Northeastern U.S. (Liebert et al. 2006). As the positive feedback cycle continues, our sites farther from Boston may come to look more similar to those near the port. This system is an intriguing case of a possible extinction vortex attributable to competition between two congeners that occupy the same niche, which helps to shed light on the processes by which invasive species cause local extinctions of natives.

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