

Intraspecific trait variation and colonization sequence alter community assembly and disease epidemics

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When individuals from multiple populations colonize a new habitat patch, intraspecific trait variation can make the arrival order of colonists an important factor for subsequent population and community dynamics. In particular, intraspecific priority effects (IPEs) allow early arrivers to limit the growth or establishment of later arrivers, even when competitively inferior on a per-capita basis. Through their effects on genes and traits, IPEs can alter short-term growth and long-term evolutionary change in single species metapopulations. Given their importance for intraspecific interactions, IPEs in a dominant species have the potential to affect the composition of entire communities. We conducted an experiment to determine whether and how arrival order and IPEs in the zooplankter *Daphnia pulex* affected its interactions with both competitors (the cladoceran *Simocephalus vetulus*) and parasites (the virulent fungus *Metschnikowia bicuspidata*). We found strong evidence for IPEs in *Daphnia*, as early arrivers inhibited late arrivers even when competitively inferior. These IPEs in *Daphnia* altered both the establishment success of interspecific competitors and the size of disease epidemics: early colonization by fast-growing *D. pulex* led to large *Daphnia* populations and low competitor establishment, but large disease epidemics. Early colonization by slow-growing *D. pulex*, on the other hand, resulted in small *Daphnia* populations with high competitor establishment, but smaller disease epidemics. Overall, our results demonstrate the importance of intraspecific variation and arrival order for community dynamics, and highlight IPEs as a general mechanism driving variation in natural communities.

In many species, early arrivers to a habitat patch gain an advantage over later arrivers in terms of resource acquisition, growth, and/or survival (e.g. amphibians: Eitam et al. 2005, bacteria: Fukami et al. 2007, plants: Moore and Franklin 2012, parasites: Hoverman et al. 2013). This influence of immigration sequence, known as an intraspecific priority effect (IPE), occurs when early arrivers limit the growth or establishment of later arrivers. IPEs can skew the distribution of genes and traits in a population toward those of early arrivers, even if early arrivers are competitively inferior on a per capita basis (de Roode et al. 2005, Ben-Ami et al. 2008). Thus, important population dynamics (e.g. growth rate) may be disproportionately represented by the traits of early arrivers, not necessarily those of all colonists (De Meester et al. 2002, Dibble et al. 2014). Previous studies indicate that IPEs can maintain long-term variation among populations in a landscape (Ventura et al. 2014), as early colonists resist subsequent immigration and the homogenizing effects of dispersal (Boileau et al. 1992, De Meester et al. 2002, Haag et al. 2006). While this clearly emphasizes the importance of assembly sequence and IPEs for intraspecific interactions, it is unclear whether variation in arrival order of a single species scales up to influence interactions between species.

Differences in assembly sequence, and IPEs in particular, have the potential to affect community assembly through

several pathways. Most directly, IPEs could alter species interactions by changing population dynamics (i.e. numerical effects). For instance, if IPEs facilitate the establishment of slow-growing individuals in a new patch (Dibble et al. 2014), the resulting reduction in population growth rate and density of a focal species could increase the invasion success of competing species. Alternatively, IPEs could affect species interactions by influencing the distribution of other important traits, such as susceptibility to parasites. IPEs that promote the establishment of highly resistant host individuals, for example, could reduce disease risk in one population, compared to neighboring patches where relatively susceptible individuals colonized early (akin to Antonovics et al. 1997). Thus, interspecific interactions like competition and parasitism may depend substantially on the traits of early arrivers of a focal species, not necessarily the traits of all colonizing individuals. Given the ubiquity of trait differentiation among local populations (Bolnick et al. 2011), IPEs may play a substantial role in community assembly.

In this study we used a model system to experimentally test whether and how IPEs in a dominant species affect intra- and interspecific interactions. We manipulated the order of arrival of individuals from two source populations to a novel habitat patch. Individuals from these populations differed in at least one key trait, population growth rate,

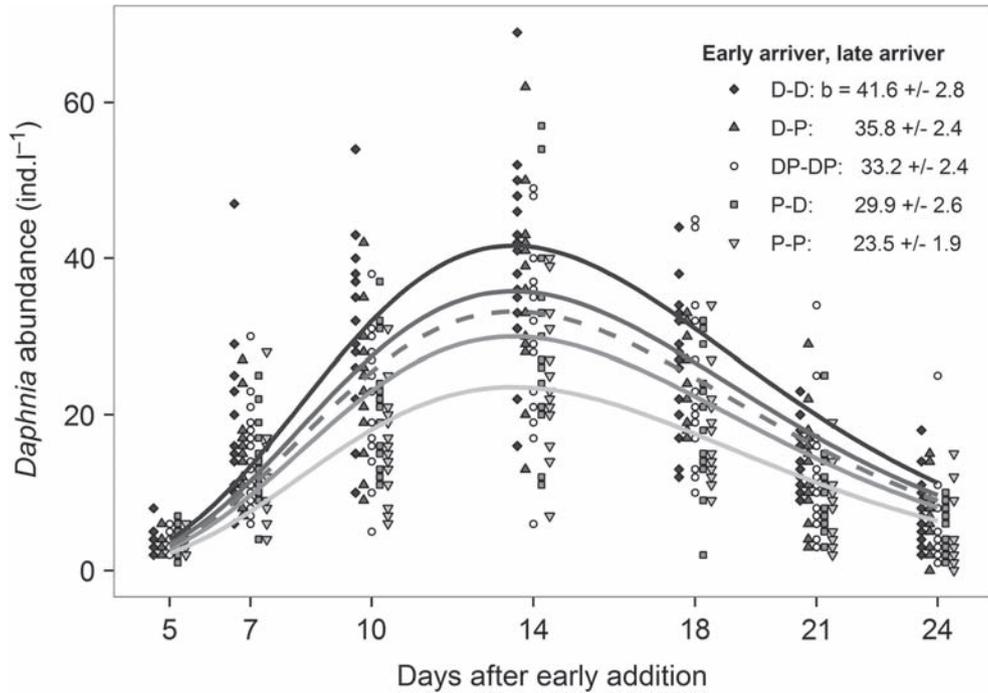


Figure 1. *Daphnia* abundance from days 5 to 25 for order of arrival treatments, showing fit to Eq. 1 with b (population performance) estimates for each treatment. Peak abundance for all populations was on day 14. All populations were sampled on the same days shown on the x-axis, but points are spaced for clarity. The simultaneous arrival treatments (DP-DP) are shown with a dashed line (and white circles). Early arrivers were introduced on day 0, parasites on day 5, late arrivers on day 7, and competitors on day 10.

which affects intraspecific competition, interspecific competition, and disease susceptibility. In a three-species system, we hypothesized that 1) variation in population arrival order would affect the population dynamics of a dominant focal species (*Daphnia pulex*) via IPEs, and that these differences in *Daphnia* populations would 2) alter interspecific competition (with *Simocephalus vetulus*), and 3) change the severity of disease epidemics (of the fungal parasite *Metschnikowia bicuspidata*) in their *Daphnia* host. Our results confirmed that variation in arrival order and IPEs altered population dynamics in *Daphnia*, and that these changes affected both competitor persistence and disease epidemic severity. These results clearly indicate that the immigration history of a single species can alter interspecific interactions, documenting the importance of intraspecific variation, arrival order, and IPEs for the development of natural communities.

Material and methods

Study system

We used the pond-dwelling zooplankton *Daphnia pulex*, the fungal parasite *Metschnikowia bicuspidata*, and the cladoceran competitor *Simocephalus vetulus* to investigate the role of variation in population arrival order and IPEs on intra- and interspecific interactions in an experimental setting. We collected populations of our focal species, *D. pulex*, from two small ponds (Ditch and Pine) in Huntsville, Texas, in February 2012. These ponds are separated by ~300 m, and dry periodically throughout the year. We hatched individuals from resting eggs (ephippia), and

then reared individuals from these two source populations separately in the lab. We kept populations under identical conditions for approximately two generations to standardize maternal or environmental effects. As individuals hatched from multiple sexually-produced ephippia (Banta 1939), these populations were polycultures, not individual clonal lineages. Though source populations were hatched from a similar number of resting eggs, grown to similar densities prior to the experiment, and treated identically in the laboratory, we made no effort to standardize genetic diversity between the two source populations in this study. These random samples (polycultures) of natural populations better reflect variability found in the field. Individuals from the Ditch population (hereafter, population ‘D’) grew to higher abundance than individuals from the Pine population (population ‘P’) under laboratory conditions (Fig. 1).

Experimental design

Our main hypothesis was that variation in the arrival order of individuals from two distinct populations of *D. pulex* would lead to IPEs, which would alter interactions with its competitor (*S. vetulus*) and fungal parasite (*M. bicuspidata*). To test this, we experimentally altered the order of arrival of *Daphnia* individuals from the two natural source populations (D and P), crossed these arrival treatments with the presence or absence of parasites, and added a heterospecific competitor to all experimental tanks. This resulted in ten total treatments (five arrival times, two parasite treatments, Table 1), replicated eight times in a randomized block design. We manipulated *Daphnia* arrival order by adding

Table 1. Order of arrival treatments for early and late additions of *Daphnia pulex* to experimental microcosms. Individuals from the two populations (Ditch, 'D' and Pine, 'P') differed significantly in population growth rates. Treatments received either individuals from single or multiple source populations, with multiple populations added either sequentially or simultaneously. All order of arrival treatments crossed with presence (+) or absence (-) of fungal parasite *Metschnikowia bicuspidata*, added on day 5. All treatments received individuals of the competitor, *Simocephalus vetulus*, on day 10. n = 8 replicates.

Early arriver (day 0)	Late arriver (day 7)	Abbreviation	Population
Ditch	Ditch	D-D	single
Pine	Pine	P-P	
Ditch	Pine	D-P	multiple 'sequential'
Pine	Ditch	P-D	
Both	Both	DP-DP	multiple 'simultaneous'

individuals from our two *D. pulex* populations at two different time points, seven days apart (day 0 = early arrival, day 7 = late arrival). We altered the identity of the early and late arrivers to create 1) 'single' population treatments, with individuals from the same source introduced during each addition, and mixed populations with 2) 'sequential' arrival treatments, where the identity of the early and late arriver differed, and 3) 'simultaneous' arrival treatments, where individuals from both source populations were added together during each colonization event (Table 1). In general, strong effects of early arriver identity (e.g. on population abundance) in mixed populations, independent of the identity of later arrivers, would be consistent with IPEs.

Daphnia were added to simple habitat patches at the same density for each addition (10 ind. l⁻¹). To reduce initial variation in population growth, we added similar size distributions of *D. pulex* to each container (1:2:1 ratio of small:medium:large). Size classes were similar between source populations (mean body length (in mm) ± SE: small, pop. D = 0.734 ± 0.019 (n = 35), pop. P = 0.800 ± 0.027 (n = 23); medium, pop. D = 1.08 ± 0.038 (n = 29), pop. P = 1.13 ± 0.040 (n = 19); large, pop. D = 1.45 ± 0.039 (n = 25), pop. P = 1.49 ± 0.043 (n = 18)). Habitat patches (microcosms) consisted of plastic containers filled with 800 ml of media (75% ADaM, Klüttgen et al. 1994, and 25% pond water filtered through 0.2 μm mesh), kept on a 16:8 hour day:night cycle at 21°C. We added 1 × 10⁴ cells ml⁻¹ of laboratory-reared algae *Scenedesmus obliquus* daily as a food source. Twice per week, we removed ~25% of each population, then counted and determined the infection status of individuals before returning them alive to their experimental container.

We added the cladoceran *Simocephalus vetulus* (7.5 ind. l⁻¹) to all of our experimental containers on day 10, representing heterospecific colonization during the initial growth phase of the focal species (*D. pulex*). Both species commonly co-occur in small ponds and temporary pools in eastern Texas (Dibble unpubl.). We collected adult *S. vetulus* from a third pond in Huntsville, Texas, in February, 2012, and raised them in the laboratory for approximately one generation before introduction to our experimental habitat patches. All *S. vetulus* used in the experiment were kept in a single source polyculture prior to experimental additions, and distributed among populations at a 1:3:1 small:medium:large ratio (mean body length (mm) ± SE:

small = 0.696 ± 0.025 (n = 29), medium = 1.06 ± 0.010 (n = 39), large = 1.46 ± 0.032 (n = 53)). Despite several laboratory trials, we have never observed *S. vetulus* infected with *M. bicuspidata* (Dibble unpubl.).

The order of arrival treatments (Table 1) were crossed with the presence/absence of the parasite *M. bicuspidata*. We did this 1) to test whether IPEs in *D. pulex* altered interactions with its parasite, and 2) because previous work has shown that the presence/absence of IPEs can depend on the presence/absence of parasites (Dibble et al. 2014). We added fungal parasite spores (40 spores ml⁻¹) to half of our habitat patches five days after the early *Daphnia* introduction. We have cultured this parasite on a variety of *D. pulex* genotypes since 2011 (and on genotypes of the host congener *Daphnia dentifera* since 2003, Hall et al. 2010). In host *D. dentifera*, *M. bicuspidata* exhibits no detectable genetic variation across its range (Duffy and Sivars-Becker 2007, Searle et al. 2015). This lack of parasite diversity, the corresponding absence of any significant response to selection (Auld et al. 2014), and our use of novel *D. pulex* genotypes likely precluded the development of particular host genotype/parasite strain associations in our experiment.

Statistical analyses

IPEs and Daphnia growth: We quantified the growth rates of our focal *D. pulex* populations by fitting a modified Ricker function (Persson et al. 1998, Bolker 2008) to population abundance data from days 5 to 24 (see Supplementary material Appendix 1 for model selection details). This period captured the peak increase, maximum abundance, and subsequent decline for all experimental populations (Fig. 1, Supplementary material Appendix 1 Fig. A1). We used the function as a phenomenological model describing the overall shape of *Daphnia* population growth. The function follows the form:

$$\text{abundance} = b \frac{x}{a} e^{\left(1 - \frac{x}{a}\right)^\epsilon} \quad (1)$$

where x is time (days), b represents the rate of initial population growth, a reflects the time (day) of peak density, and ε changes the steepness (kurtosis) of the curve (Fig. 1). For our experimental populations, allowing a and ε to vary by treatment did not increase the fit of the model (based on AIC, Burnham and Anderson 2002). We thus focused our analyses on population growth, b. Because a and ε were held constant, b modifies the entire growth curve, encompassing initial growth rate, peak population density, and subsequent population decline. In our study, then, b represents an aggregate measure of population growth or performance throughout the experiment, and is not simply a transient rate of increase. We estimated b for each of our experimental units (microcosms), and used this estimate of population performance in subsequent analyses. Weighting b by the standard error of its estimation did not qualitatively alter our results, and we present models and results with unweighted estimates.

Factorial models

Our statistical models all took the same general approach. We tested whether altering the order of arrival of individuals from

our two source *D. pulex* populations affected 1) *Daphnia* population performance (i.e. *b*, growth and peak density), 2) competitor establishment success (persistence until the end of the experiment, binary), and 3) disease epidemic severity (infection prevalence integrated over the entire duration of the experiment) using generalized linear mixed effects models (glms). We included fixed effects of early arriver identity, late arriver identity, parasite presence, and all possible interactions of these factors, plus a random effect of spatial block. For these factorial models, we did not include the simultaneous arrival treatments, because they were not implemented factorially. For each model, we performed model selection by minimizing AIC (Burnham and Anderson 2002, see also Supplementary material Appendix 1 Table A3–A5). We made pairwise comparisons between all treatments (including simultaneous arrival treatments) for models of *Daphnia* population growth and disease epidemic severity, correcting for multiple comparisons by controlling the false discovery rate (Benjamini and Hochberg 1995). *Daphnia* growth (*b*) was modeled with a normal error distribution, *Simocephalus* establishment success with a binomial, and disease epidemic severity with a negative binomial distribution to account for overdispersion (Ver Hoef and Boveng 2007). Statistical significance was assessed via F-tests for models with normally distributed error (*Daphnia* population performance), with an approximation to denominator degrees of freedom (Kenward and Roger 1997). For models with non-normal error (*Simocephalus* establishment, epidemic severity) we computed significance via Wald χ^2 -tests.

All statistical analyses were performed in R (<www.r-project.org>). All mixed effects models were fit via the lme4 package (Bates et al. 2014), with AIC values, summary statistics, post hoc comparisons, and figures generated with the packages bbmle (Bolker 2009), car (Fox and Weisberg 2011), multcomp (Hothorn et al. 2008), and ggplot2 (Wickham 2009), respectively.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.124n0>> (Dibble and Rudolf 2015).

Results

Daphnia population dynamics

The population identity of the early and late arrivers significantly altered *Daphnia* performance (early, $F_{1,53} = 26.9$, $p < 0.0001$; late, $F_{1,53} = 7.15$, $p = 0.0096$; Fig. 1, 2a, see Supplementary material Appendix 1 Table A3 and A4 for model selection and full model summary). Parasite presence did not significantly alter *Daphnia* population performance ($F_{1,53} = 0.50$, $p = 0.48$), despite substantial disease epidemics. There were no significant interactions between arrival order treatments and parasite presence (Supplementary material Appendix 1 Table A4). In the single population treatments, differences between populations D and P were substantial, with D populations peaking on average at 76% higher densities than P populations (Fig. 1, 2a; D-D > P-P, $p < 0.0001$).

Our paired comparisons showed that replacing early P (from the P-P treatments) with early D resulted in a 52%

mean increase in peak density (Fig. 1, 2a; D-P > P-P, $p < 0.001$). On the other hand, replacing early D (from the D-D treatments) with early P reduced average peak density by ~38% compared to D-D (Fig. 1, 2a; P-D < D-D, $p < 0.01$). These comparisons demonstrate the strong influence of early arriver identity, which drove the growth rate, peak density and subsequent decline of colonizing populations (see also Table 2).

The sequential arrival treatments (Table 1) showed moderate differences in peak density (~19%, D-P \geq P-D, $p = 0.073$). Simultaneous arrival treatments resulted in intermediate growth: 40% larger than the slowest-growing, least abundant populations (Fig. 2a; DP-DP > P-P, $p < 0.005$), 25% smaller than the fastest-growing, most abundant populations (DP-DP < D-D, $p < 0.05$), and virtually identical to the sequential arrival treatments (Fig. 2a; DP-DP versus D-P, $p = 0.418$; DP-DP versus D-P, $p = 0.325$).

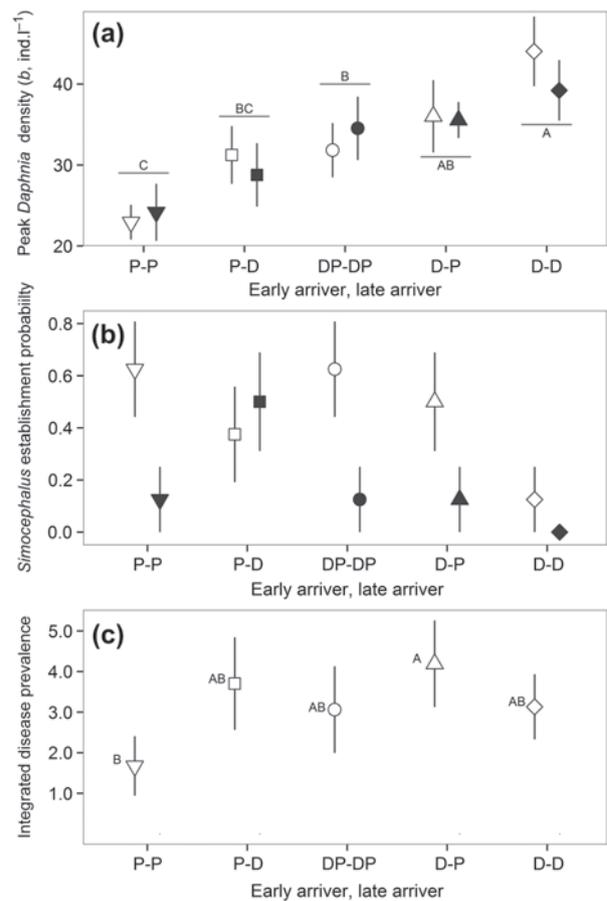


Figure 2. (a) Treatment means \pm 1 SE for *Daphnia* population performance (*b* – peak density, Eq. 1), by order of arrival treatment. Arrival treatments sharing a letter are not significantly different after correcting for multiple comparisons (FDR); because there was no effect of parasites on peak density (*b*), comparisons ignored parasite presence. (b) *Simocephalus* establishment probability (i.e. successful persistence until the end of the experiment) as a function of *Daphnia* arrival order and parasite presence. Treatments are ordered as in panel (a); solid shapes are parasite-free, hollow shapes are parasite-addition. (c) Integrated disease prevalence (mean \pm 1 SE) for each *Daphnia* order of arrival treatment. Treatments sharing a letter are not significantly different after correcting for multiple comparisons (FDR).

Table 2. The effect of replacing host *D. pulex* individuals from one source population (Ditch or Pine) with individuals from the other at different arrival times. Shown is the mean percent change for the relevant replacement, calculated as (replacement – original) / original, for each of host (*D. pulex*) abundance (*b*), competitor (*S. vetulus*) establishment success, and disease (*M. bicuspidata*) epidemic severity (infection prevalence integrated through time). As parasites had no effect on host abundance, percent change is pooled across treatments with and without parasites. *indicates raw difference in proportion of populations in which *S. vetulus* established successfully, as the percent change is undefined (competitor completely excluded from D-D host populations without parasites).

Effect of replacing:	P -> D				D -> P			
	Early (i.e. P-P to D-P)		Late (P-P to P-D)		Early (D-D to P-D)		Late (D-D to D-P)	
Arrival time	absent	present	absent	present	absent	present	absent	present
Parasites								
Percent change in:								
Host abundance	52.00%		27.40%		-28.00%		-14.10%	
Competitor est.success	0.00%	-20.00%	300.00%	-40.00%	50%*	200.00%	12.5%*	300.00%
Disease epidemic size	-	150.90%	-	121.56%	-	18.21%	-	33.87%

IPEs and interspecific competition

Daphnia order of arrival treatments significantly altered *Simocephalus* establishment. Specifically, the probability of *Simocephalus* persisting in the community was strongly affected by the identity of early arriving *Daphnia* (Wald $\chi^2 = 4.16$, $n = 60$, $p < 0.05$), and there is evidence that an interaction between late arriver identity and parasite presence played a lesser role (Wald $\chi^2 = 3.66$, $n = 60$, $p = 0.056$, see also Supplementary material Appendix 1 Table A5). The effect of early arriver identity reflects lower *Simocephalus* establishment success when fast-growing *Daphnia* individuals colonize first (18.75% with early D arrival, 40.6% with early P arrival). In general, *Simocephalus* showed a higher likelihood of persistence when parasites were present (Fig. 2b, open versus closed symbols). This was not the case, however, when fast-growing *Daphnia* arrived late. In the P-D and D-D order of arrival treatments, parasite presence did not affect *Simocephalus* establishment (though the difference is trivial for the D-D arrival order, because *Simocephalus* only established successfully in 1/16 habitats).

IPEs and disease epidemics

Disease epidemic severity (i.e. infection prevalence integrated over time), was affected by a significant interaction between early and late arriver identity (early \times late, Wald $\chi^2 = 6.51$, $n = 29$, $p = 0.0108$). This indicates that late arrival of D individuals led to similarly sized epidemics regardless of early arriver identity, while the effect of late P depended on the identity of the early arriver (Fig. 2c). A more general explanation, however, is that epidemic severity tended to be high whenever D individuals were present in the population. Pairwise comparisons show that epidemic size doubled in D-P populations compared to P-P populations (D-P > P-P, $p < 0.05$). Other treatments showed similar epidemic sizes, including the simultaneous arrival treatments (pairwise comparisons, $p > 0.05$). Overall, disease epidemic severity was positively related to peak host density (Supplementary material Appendix 1 Fig. A3, Table A7).

Summary

Changing the identity of early and late *D. pulex* colonizers tended to create different ecological communities (Table 2). For instance, communities receiving slow-growing *Daphnia*

both early and late harbored small *Daphnia* populations, which facilitated competitor establishment success and inhibited large disease epidemics (Fig. 2). Had fast-growing *Daphnia* arrived first (i.e. a shift from P-P to D-P), however, we would expect *Daphnia* populations to be approximately 52% larger, with a 20% reduction in the establishment success of *S. vetulus*, and a 150% increase in disease epidemic severity (on average, for communities with parasites, Table 2).

Discussion

Intraspecific priority effects (IPEs) occur when early arrivers to a habitat patch affect the establishment or growth of later arriving conspecifics (Boileau et al. 1992, De Meester et al. 2002, Dibble et al. 2014), but whether and how they influence interspecific interactions remains unclear. Consistent with previous studies, we found that IPEs played an important role in driving population dynamics of a focal species. However, our results extend previous findings by demonstrating that these differences alter colonization success of an interspecific competitor as well as the size of disease epidemics. Thus, our study provides one of the first clear examples demonstrating that IPEs in a single species can have strong consequences for the structure and dynamics of natural communities.

IPEs and intraspecific dynamics

Our source populations of *Daphnia pulex* exhibited substantial variation in growth rate, individuals from the Ditch (D) source population achieving peak density almost twice that of Pine (P) in single population treatments (Fig. 1). This variation among single populations established expectations for these populations in mixture. If early and late arrivers were independent, we would expect that overall population dynamics (e.g. peak population size) would be driven predominantly by population D, independent of their arrival order. Instead, we found that the identity of the early arriver significantly altered *Daphnia* population dynamics, even when individuals from population P colonized first. Populations with early P, late D, for example, reached lower peak densities than early D, late D, indicating that early P reduces population performance compared to early D. In other words, the late arrival of individuals from a faster-growing population

did not ‘save’ these slow-growing populations from the reduced density associated with traits of the early arriver (i.e. *D. pulex* abundance statistically similar in P-P and P-D treatments). All populations had similar abundance after this initial growth and peak (Supplementary material Appendix 1 Fig. A1), indicating that early P, late D did not simply peak later. In this case, the substantial influence of slow-growing early arrivers represents an IPE. In our sequential treatments, however, we saw a more moderate (19%) difference in *D. pulex* density between populations (D-P \geq P-D) that approached statistical significance ($p = 0.073$). Thus, early arrivers did not completely eliminate the influence of late arrivers. Our experimental results for *D. pulex* abundance parallel previous work in other systems, where weaker competitors (i.e. slower growers) can gain an advantage by early colonization (de Roode et al. 2005, Dibble et al. 2014). While we cannot conclusively state that late arriver establishment success was lower in our experiment without genotypic data, the influence of arrival order and IPEs had clear effects on an aggregate measure of population performance (*b*), and hence had the potential to alter interspecific interactions.

IPEs and interspecific dynamics

We found strong effects of *Daphnia* arrival order on competitor establishment, indicating that IPE-mediated differences in *Daphnia* population extended to alter their interspecific interactions. When *Daphnia* from the Ditch (D) population arrived early, they more effectively reduced the establishment success of the competitor *Simocephalus vetulus*, completely excluding *S. vetulus* from a number of communities. *Simocephalus* is generally a weaker competitor than *Daphnia*, in terms of growth rate, abundance, and total biomass (Schwartz and Hebert 1989, Louette and De Meester 2007). Our results, though, show that IPEs in *Daphnia* can facilitate *Simocephalus* establishment. Particularly, when slower-growing *Daphnia* from the Pine (P) population gained an advantage by arriving early to a new habitat patch (e.g. P-D versus D-D, Fig. 2b, see also Supplementary material Appendix Fig. A2), *Simocephalus* were more likely to persist in the community. In other words, the establishment success of a given species depends not only on the presence of a competitor, but also the order in which competitor individuals colonize a habitat.

Additionally, we found a positive effect of parasites on *Simocephalus* establishment. This parallels previous work showing that selective predation on *Daphnia* increases *Simocephalus* abundance in communities (Schwartz and Hebert 1989). In our case, however, parasites did not reduce *Daphnia* density. There is preliminary evidence that exposure to parasite spores reduces *Daphnia* foraging behavior (S. R. Hall unpubl.), and heavily infected *Daphnia* eventually stop foraging altogether (due to mechanical inhibition by parasite spores, Hall et al. 2009). Changes in foraging behavior resulting from parasites could reduce the per capita competitive ability of *Daphnia*, increasing establishment success of *Simocephalus*. Parasite spillover from *Daphnia* to *Simocephalus*, which we would expect to reduce *Simocephalus* growth or establishment, is extremely unlikely, given that repeated laboratory trials have failed to infected

S. vetulus with *Metschnikowia bicuspidata*. Thus, a more general parasite (such as *Spirobacillus cienkowskii*, Ebert 2005) might give rise to more complex dynamics between hosts, their parasites, and their competitors. Overall, both variation in the arrival order of individuals from distinct *Daphnia* populations and the presence of parasites affected the likelihood of *Simocephalus* persistence.

IPEs in *Daphnia* populations also significantly altered host-parasite interactions and the severity of disease epidemics. Epidemics were largest in D-P arrival treatments (Fig. 2c), and the difference in epidemic size between D-P and P-P populations reflects an IPE, as these treatments also differed in *Daphnia* population density (D-P > P-P). In this case, early D increased peak host population density (compared to early P), but at the cost of higher disease burden. On the other hand, P-D arrival treatments reduced *Daphnia* population density compared to D-D treatments, consistent with an IPE reducing host population size. With density-dependent disease transmission, this should have significantly reduced the severity of disease epidemics. Epidemic size was similar, however, in P-D and D-D treatments (although epidemics in P-D populations appeared to peak later in the experiment, Supplementary material Appendix Fig. A1). This similarity suggests that differences in peak population density alone cannot explain differences in epidemic severity, and that other traits may be involved.

Aside from substantial differences in population growth, our two source populations of host *D. pulex* likely differed in a number of traits. Due to tradeoffs between fecundity and disease susceptibility, it is possible that individuals from the faster-growing, high-performing D population were more susceptible on average than P individuals (Hall et al. 2010, 2012, Dibble et al. 2014). Differences in individual susceptibility could have produced similarly-sized epidemics despite differences in peak host density. These tradeoffs are not ubiquitous, however, as their presence or absence depends on environmental conditions (Hall et al. 2012), and mean per spore susceptibility (a component of overall disease risk) does not necessarily scale with foraging rate or population growth (Auld et al. 2013). Thus, differences in mean per spore susceptibility, which we did not measure, independent of foraging or fecundity traits could have contributed to our observed patterns of disease epidemic severity. Additionally, enhanced genotypic richness in *Daphnia* populations is known to increase overall resistance to parasites (Altermatt and Ebert 2008), though the effects seem to be stronger when multiple parasite genotypes are present (Ganz and Ebert 2010). Although we treated source populations identically, we did not standardize genotypic richness. Our results are generally consistent with observed tradeoffs between disease risk and fecundity, but we cannot rule out these other possible drivers of host/parasite dynamics.

Overall, we found that differences in arrival order and IPEs in *Daphnia* populations led to ecologically divergent communities (Table 2). Early arrival of slower-growing *Daphnia* (i.e. Pop. P) resulted in smaller *Daphnia* populations and smaller disease epidemics, but a higher likelihood of competitor persistence. Early arrival of faster-growing (Pop. D) *Daphnia* led to large populations that more effectively inhibited competitors, but at the cost of larger disease epidemics. A number of studies document

the importance of intraspecific variation for assemblages of multiple species (Fridley and Grime 2010, Crawford and Rudgers 2013, Crutsinger et al. 2014). However, these studies generally focus on ‘who’ is present in an environment (i.e. which individuals, genotypes or ecotypes of a species). Our results suggest that community development and structure may not only depend on who gets to a habitat, but also ‘in what order’ they get there. Thus, IPEs may play a major mechanistic role in the interspecific dynamics of metacommunities.

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Supplementary material (available online as Appendix oik.02373 at <www.oikosjournal.org/readers/appendix>). Appendix 1. Additional methodological details, model selection and summary statistical tables, and analyses of *Simocephalus* establishment and disease epidemic severity by *Daphnia* population performance (*b*).

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