

The effect of environment-dependent dispersal rate on the relative abundance of native and nonnative snails

Robin R. Decker

Center for Population Biology, University of California, Davis, California 95616 USA

Abstract.

Dispersal rate, which often is greater in nonnative species, has been shown to effect population abundance in studies of single species. While there is much focus on native and nonnative species that compete in communities, as well as how interactions between native and nonnative species will adjust with climate change, we need a better understanding of how environment-dependent dispersal rates affect multispecies population abundances in a changing climate. In this study, I measured the movement rate of two species of snails, one native and one nonnative, in two different environments: damp, cool and warm, dry. Native snails move slower than nonnative snails, and snails in dry environments move faster than snails in damp environments. I used these movement rates to parameterize a simulation of native and nonnative snail population dynamics in a patchy habitat. Additionally, I explored how relative differences in dispersal between snail species in damp environments and dry environments, which are more likely to be found with climate change, affect population abundances. Nonnative snails always have higher abundance in these simulations, due to their high dispersal rates. The relative amount of change in dispersal probability affects how abundances may change with climate: population abundances of native and nonnative are more disparate when the relative difference in dispersal rates between species is greater. These results suggest environment-dependent dispersal rates, which will change with climate, will change the relative abundance of native and nonnative species, but the direction of the change is dependent on the magnitude of dispersal difference. The way in which relative environment-dependent dispersal abilities in competing species affects their abundances is an essential mechanism predicting how species interactions will change with climate.

Key words: exotic species, climate change, simulation, dispersal, population dynamics

INTRODUCTION

The rate at which an organism moves can have profound effects on its population dynamics (Amarasekare 1998) as well as its interactions with other species. The fact that species exist in space and disperse in their environments to interact has widespread consequences for the population dynamics of all species in a community (Kareiva et al. 1990), even those that do not disperse or disperse less. With the recent increase in habitat invasions by exotic species (Sakai et al. 2001), quantifying the relative dispersal rates of invasive species compared to the natives with which they compete, as well as understanding the effects of differences in dispersal dynamics in species, is critically important. Increased dispersal ability helps invasive species spread, and therefore recent management efforts have focused on investigating the factors that lead to faster dispersal in invasive species, ways to decrease invasive dispersal rates and ways to increase native dispersal (Andrew & Ustin 2010).

Climate change is already restructuring communities, changing the way that species interact, and is predicted to continue to alter species interactions and population dynamics (Graham & Grimm 1990), though the direction of these changes is often uncertain and system-dependent. Particularly, climate change may impact the transport, establishment, abundance, distribution and effectiveness of control measures of nonnative species (Hellmann et al. 2008), which all indirectly impact the natives that co-occur with these species. Climate change may directly affect dispersal ability of both native and nonnative organisms, but in which direction is not clear. Exotic species may gain increased dispersal ability under global warming, while native dispersal decreases, or the opposite trend may occur. It is also possible that both will suffer under climate change, or both will increase in dispersal ability. In this case, the relative increase or

decrease in dispersal rates may put natives or exotics at an advantage over the other. The way that dispersal affects population dynamics may even change with the warming climate.

Therefore, we need to both empirically investigate and mathematically model the effects of changing climate on the way dispersal impacts population dynamics of native and nonnative species.

Native and nonnative terrestrial snails coexist throughout most of California. Using snail movement rates as a proxy for dispersal rates, we can compare the ability of native and nonnative snails to disperse. Snail movement is relatively slow, making measurement tractable. Additionally, snails can easily be transported to a variety of environments, some drier and warmer, as they may experience under climate change. Therefore, snails are an ideal study system for testing for different dispersal abilities in different environments among both native and exotic species. While examining the effect of dispersal differences on population dynamics may be difficult in snails, mathematically modeling this effect can easily be done via simulation. Snails live in patchily distributed plants, so simulating a model of patch dynamics may be more realistic for these species than others that are more heterogeneously distributed.

The objectives of this study are to (1) test for differences in movement rate in native and nonnative snails in dry, warm environments and wet, cool environments, (2) determine how these empirically derived differences in movement translate to differences in relative abundance of the two species and (3) analyze how different scenarios of changing dispersal rates with climate change affect relative increases or decreases in native snail abundance. These objectives will not only inform us how native and nonnative snail abundance may change under global warming, but also reveal mechanistically how dispersal differences affect population dynamics.

METHODS

Study system

I conducted this study at the University of California Bodega Marine Reserve (38°19' N, 123°3' W). Two snail species co-occur in Bodega Bay, the exotic species *Cornu aspersum* (formally *Helix aspersa*), the common garden snail, which is native to Mediterranean regions in Europe, but currently is cosmopolitan in temperate regions globally, and the native species *Helminthoglypta arrosa*, the bronze shoulderband snail. Both species are nocturnal, and increase their activity during the rainy season in winter through spring (Van der Laan 1791). I collected eight nonnative snails and six native snails from patches of calla lilies (*Zantedeschia aethiopica*), which are exotic species in North America, native to parts of Africa (Kuehny 2000). The mean size (diameter of shell) of native snails collected was 1.9 cm and the mean size of nonnative snails collected was 2.3 cm.

Snail dispersal experiments

I conducted the snail dispersal experiments in late March, 2015 in the area directly outside and southeast of the Bodega Marine Laboratory. To measure snail movement, I placed four meter sticks meeting at 90 degree angles on relatively flat areas of ground that were spotted with grasses and small plants. Each snail was placed one at a time at the origin of these meter sticks, the location where the four meter sticks met, and the position of the snail was recorded every ten seconds for five minutes, for a total of thirty measurements of position traveled in each trial. I performed this process 14 times, once for each snail, in two different environmental conditions: wet/cool conditions and dry/warm conditions. One set of trials was performed in early in the morning, on damp ground, in the shade, in cool ambient temperature (approximately 10 to 15 degrees Celsius), and the other in the early afternoon, on dry ground, in direct sunlight and warm ambient temperature (approximately 20 to 25 degrees Celsius).

From this data, I derived estimates of total distance each snail moved in each environment, by summing the distances moved in each ten second interval. This resulted in two treatments (snail species and environment), which affect the distance the snail moved in the allotted five minutes. The data was not normally distributed, so I used the Van der Waerden normal scores test in the *agricole* package in R (de Mendiburu 2014), a nonparametric statistic, to determine differences in total snail movement.

Snail population dynamics simulation

To determine if snail movement rates can have an effect on population dynamics, I conducted a simulation experiment. In this simulation, I assumed snails occupy discrete habitat patches, similar to the calla lilies, which grow in groups of clusters. I used 20 patches in each simulation, 10 of which were initially occupied, and 10 of which were initially unoccupied. I generated the initial abundances of native and nonnative snails in each occupied patch from a normal distribution with mean 10 and standard deviation 2, so that, on average, each occupied patch contained 10 native snails and 10 nonnative snails.

At each time step, each snail has a probability of giving birth to one new snail, a probability of dying, and a probability of moving to another patch that with a lower total population than the patch in which it currently resides. Specifically, in each time step, the snail decides if it will move based on its assigned movement probability. If that decision is to indeed move, it randomly moves to any patch with a lower population than its own. By using this method, snails will diffuse from areas of high snail concentration to areas of low snail concentration. The probabilities of birth, death and movement are included in Table 1. Note that birth rates are the same in both snail species, as well as death rates. The only differences between species are in movement probabilities.

I assume that each patch has a carrying capacity of 100 total snails. When a patch has 100 snails, no new snails can be born in that patch, but adults currently occupying a full patch may move to other patches that still have room. When adults leave a full patch, more room becomes available for new snails to be born in that patch again, or snails from other patches to move in. The simulation continues until all patches are at carrying capacity. Then, the number of native snails and nonnative snails in each of the 20 patches is recorded.

This procedure was performed 100 times for parameters representing the cool, wet environment and 100 times for parameters representing the warm, dry environment. These probabilities of moving are proportional to the empirically determined total distance moved in each environment for each snail, as found in the snail dispersal experiments outlined. The exact movement probability parameters used for native and nonnative snails in wet and dry environments are located in Table 1.

Statistical Analysis of Simulation Data

I used a Bayesian statistical inference framework to test for different population levels in natives and nonnatives in the dry environment versus the wet environment, employing Markov chain Monte Carlo methods, using the Stan language (Stan 2013, Stan 2014). Using Stan, I fit four different models: one with the main effects of species, environment type and the interaction of species and environment type, one with only the two main effects of species and environment, one with just the main effect of environment and one with just the main effect of species. I used Akaike Information Criterion (AIC) to choose the best-fit model of those I tried. The models used are summarized in Table 2.

Sensitivity of population dynamics to movement parameters

To first test if the ratio of movement rate parameters (native movement in dry environments, native movement in wet environments, nonnative movement in dry environments, nonnative movement in wet environments) or the actual value of rate parameters affects relative abundances of snails, I ran the simulation again, changing the probabilities of movement, but keeping them in the same ratio (Table 3). Then, I tried three other combinations of movement parameters to test effects on population dynamics, repeating the entire simulation each time. First, I increased the difference in native and nonnative movement rates in dry environments compared to wet environments. Second, I increased the difference in native and nonnative movement rates in wet environments compared to dry environments. Third, I made the difference between natives and nonnatives the same in both wet and dry environments (Table 3). I fit the model with the two main effects of species and environment with interaction, using Bayesian inference, as described above, to each new set of data generated by these new parameter combinations.

RESULTS

Influence of species and environment on movement rate

The total distance moved in five minutes by the natives in wet environments, the natives in dry environments and the nonnatives in wet environments was less than the total distance moved in five minutes by the exotics (Van der Waerden normal scores test, chi square = 9.6383, $p = 0.022$, $\alpha = 0.05$, Fig. 1). Stated differently, the exotics in dry environments moved significantly more than the natives in both environments. There was no statistical difference in movement between natives in dry and wet environments.

Effects of differences in movement rates on population dynamics

The mean of the abundance of exotic snails in the wet environment was approximately 60, which was higher than the mean of the abundance of the native snails in the wet environments, which was 40 (Fig. 2). The difference in population abundance between exotic and native snails decreased in the dry environment (Fig 3). The mean population abundance of exotic snails in the dry environment was approximately 55, which was still higher than the mean of the abundance of the native snails at 45, but by a smaller margin (Fig. 2). The variance in the dry environment visually appears to be less than the variance in the wet environment (Fig. 2).

Sensitivity of population dynamics to movement parameters

Qualitatively, there was no difference in population abundance from changing the values of the movement probability parameters, but maintaining them in the same ratio (compare Fig. 3A to 3B). In both cases, exotic snails always had higher abundances, but the difference in abundance between nonnative and native snails was lower in the dry environment.

In the three treatments used to compare other combinations of movement parameters, in all cases, nonnative abundance was always higher than native abundance. Increasing the difference in native and nonnative movement rates in dry environments compared to wet environments led to an increase in the difference in abundances between native and nonnatives in dry environments compared to wet environments (Fig. 3C). Similarly, increasing the difference in native and nonnative movement rates in wet environments compared to dry environments lead to a decrease in the difference in abundances between native and nonnatives in dry environments (Fig. 3D). When differences in movement rate between natives and nonnatives were the same in wet and dry environments, the difference in abundances between native and nonnatives in dry environments decreased compared to wet environments (Fig 3E). In cases where the overall

difference in abundance between native and nonnatives in dry environments, the variance in abundances also appeared to decrease.

DISCUSSION

Increasingly, studies are confirming that climate change alters the mechanisms that control species interactions and population abundances (Graham & Grimm 1990). By using movement rate in dry, warm environments as a proxy for dispersal distances under climate change, this study is no exception to the trend.

The total amount of distance moved by native snails was significantly different than the total amount of distance moved by exotic snails in the dry environment. Even though there were no other significant differences, I used the mean distance traveled by each group to parameterize my simulation. While not all of the differences were significant, the sample size of 14 snails lacked statistical power, and with more snails measured, more significant differences may have emerged. If we do assume that native snails in wet environments move less than native snails in dry environments, which move less than exotic snails in wet environments, which move less than exotic snails in dry environments, there are several possible explanations for the pattern. While previous studies (Snider, 2007) have noted that smaller snails are capable of moving faster than larger snails, this was not the pattern observed in this study: native snails, which were smaller, on average, than nonnative snails, moved slower. This difference may be due to physiological difference in the snail. Snails in wet environments moved slower than snails in dry environments. Snails increase in abundance in areas with more shade, are limited more by shade than by food (Huntzinger et al. 2008), which suggests that snails move towards areas where shade is more prevalent. In the shady, damp, cool environment, snails may have moved slower because the environment they were in was more suitable than the dry, warm environment in full sunlight.

The faster speeds seen in the dry, warm environment may be representative of snails deciding to exit an unsuitable habitat as quickly as possible.

In all simulations conducted, nonnative snails always had higher abundances than native snails, in both wet and dry environments. Since the only parameters that changed value were movement probabilities between patches, this difference is attributable to differences in movement rates in the two species. Two aspects of the model likely lead to differences in abundances between species. Firstly, since nonnative snails are more likely to move to new patches, they are more likely to reach new patches first and subsequently grow exponentially. When native snails arrive later to patches already occupied by nonnative snails, many native snails are already present. Both species then continue to grow exponentially, but the higher initial abundance of nonnative snails puts them at an advantage. Second, imposing a carrying capacity on patches is critical in this experiment. The fact that nonnative snails colonize new patches first would not matter if patches could support an infinite supply of snails. If this were the case, native snails would grow exponentially in a small cluster of local patches, and exotic snails would grow exponentially, but more spread out over a greater area. The carrying capacity puts native snails at a disadvantage, because they reach maximum population in the patches they occupy quicker than the nonnative snails that are spread out over many patches.

Using the empirically derived movement parameters, native snails do relatively better in dry environments than wet environments, though their abundances are still lower than nonnative snails'. If the wet environment represents climate prior to climate change and the dry environment represents climate after, this indicates that climate change may be beneficial for native snails. The relative ratios of the growth parameters are critical though in this model. While shifting the movement parameters up or down in parameter space, but maintaining their ratio, has

little impact on snail abundances (Fig. 3A and 3B), changing the ratio of parameters has a profound impact on population dynamics. If both species of snail move relatively the same rate prior to climate change, but nonnative snails move much faster than natives with climate change, the native species will see great declines in abundance (Fig. 3C). Conversely, if exotic snails move much faster than native snails prior to climate change, but differences in movement rate diminish after climate change, native snails will do better after climate change, but still not as well as exotic snails (Fig. 3D), as seen in the simulation using empirically-derived parameters (Fig. 3A). Finally, in this scenario, if the difference between movement rates in native and nonnative snails in the wet environment is equal to the difference between rates in the dry environment, the native snails still do marginally better after climate change, though their abundances are still lower than those of nonnative snails. This is likely because the ratio of nonnative to native snail movement in the dry environment in this scenario is lower ($8:6 = 4:3$) than the ratio of nonnative to native snail movement in the wet environment ($4:2$), even though the absolute differences are equal. Therefore, the ratio of snail movement rates is critically important in this experiment, determining snail population dynamics.

Since the empirically derived movement probabilities are uncertain, due to small sample size, the result that native snails may increase in abundance with climate change is questionable. Collecting more data on snail movement rates will improve estimates of the impact of dispersal ability on population abundance of native and nonnative snails post climate change.

Nonnative species, once established in an area, can spread quickly, overwhelming the natives with which they compete (Sakai et al. 2001). To protect native species and thereby preserve biodiversity, there is much concern about the extent of the effect that nonnative species will have on natives, and how their interactions will change with a warming climate (Graham &

Grimm 1990). I have shown that relative dispersal rates can impact the abundance of native and nonnative species, provided evidence that movement rates of organisms may change with climate, and shown that changes in relative dispersal probabilities affect relative population abundances. However, more work needs to be done to empirically test the results of the simulations presented, and to measure dispersal rates in other native species and the invasive, exotic species with which they compete. This study demonstrates that dispersal rates alone can affect relative population abundances of two co-occurring species, even when birth rates, death rates, and initial population abundances are held equal. Environmentally-dependent dispersal rates in both native and nonnative species may be a key mechanism in understanding how climate change alters species interactions.

LITERATURE CITED

- Amarasekare, P. (1998). Interactions between local dynamics and dispersal: Insights from single species models. *Theoretical Population Biology*. 53: (44).
- Andrew, M. E., and Ustin, S. L. (2010). The effects of temporally variable dispersal and landscape structure on invasive species spread. *Ecological Applications* 20: (593).
- Graham, R. W. and Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. *Trend in Ecology & Evolution* 5: (289).
- de Mendiburu, F. (2014). *Agricolae: Statistical Procedures for Agricultural Research*. R package version 1.2-1. <http://CRAN.R-project.org/package=agricola>
- Hellmann, J. J., Byers, J. E., Bierwagen, B. G., and Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology* 22: (534).
- Huntzinger, M., Karban, R. and Cushman, J. H. (2008). Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology* 89: (1972).
- Kareiva, P., Mullen, A. and Southwood, R. (1990). Population dynamics in spatially complex environments: Theory and Data [and Discussion]. *Phil. Trans. R. Soc. B*. 330: (175).
- Kuehny, J. S. (2000). Calla history and culture. *Hort. Technology*. 10: (256).
- McElreath, R. (2014). *Rethinking: Statistical Rethinking book package*. R package version 1.47.

- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N. and Weller, S. G. (2001). The population biology of invasive species. *Annual Reviews* 32: (305).
- Stan Development Team (2013). Stan Modeling Language User's Guide and Reference Manual, Version 2.6.0 URL <http://mc-stan.org/>.
- Stan Development Team (2014). Stan: A C++ Library for Probability and Sampling, Version 2.6.0 URL <http://mc-stan.org/>.
- Snider, S. B. (2007). Towards a movement ecology: Modeling the behavioral response of invasive snails to resources and competition. Dissertation. North Carolina State University, Raleigh, North Carolina, USA.
- Van der Laan, K. L. (1971). The population ecology of the terrestrial snail *Helminthoglypta arrosa* (Pulmonata: Helicidae). Dissertation. University of California, Berkeley, California, USA.

TABLES & FIGURES

Table 1. Values of all parameters used in the initial simulation of population dynamics. The movement probability parameters are in the same ratio as the empirically derived total distances moved in five minutes.

Parameter	Parameter Value
Birth rate, native snails	0.50000
Birth rate, nonnative snails	0.50000
Death rate, native snails	0.10000
Death rate, nonnative snails	0.10000
Movement rate, native snails, wet environment	0.16560
Movement rate, nonnative snails, wet environment	0.63341
Movement rate, native snails, dry environment	0.39031
Movement rate, nonnative snails, wet environment	0.82927

Table 2. Structure of all models fit with MCMC and resulting AIC scores and AIC weights.

Model	wAIC	Weight
population = species + environment + species · environment	62854.7	1
population = species	63177.1	0
population = species + environment	63179.5	0
population = environment	65542.8	0

Table 3. Movement probability parameters for native snails and exotic snails in wet/cool and warm/dry environments for five different parameter sets. Each parameter set corresponds to resulting data and model plotted in panels of Fig. 3.

Parameter set description	Corresponding panel in Fig. 3	Movement parameter	Parameter Value
Empirically based ratio of values, shifted to higher range	B	Native snails, cool/wet environment	0.1997
		Native snails, warm/dry environment	0.4707
		Nonnative snails, cool/wet environment	0.7638
		Nonnative snails, warm/dry environment	1.0000
Large difference between native and nonnative movement rates in dry environment	C	Native snails, cool/wet environment	0.1000
		Native snails, warm/dry environment	0.2000
		Nonnative snails, cool/wet environment	0.3000
		Nonnative snails, warm/dry environment	0.9000
Large difference between native and nonnative movement rates in wet environment	D	Native snails, cool/wet environment	0.1000
		Native snails, warm/dry environment	0.7000
		Nonnative snails, cool/wet environment	0.8000
		Nonnative snails, warm/dry environment	0.9000
Difference between native and nonnative movement rates is equal in both environments	E	Native snails, cool/wet environment	0.2000
		Native snails, warm/dry environment	0.4000
		Nonnative snails, cool/wet environment	0.6000
		Nonnative snails, warm/dry environment	0.8000

Figure 1. Total distance moved by natives and exotics in wet and dry environments. Significant differences are indicated by a and b.

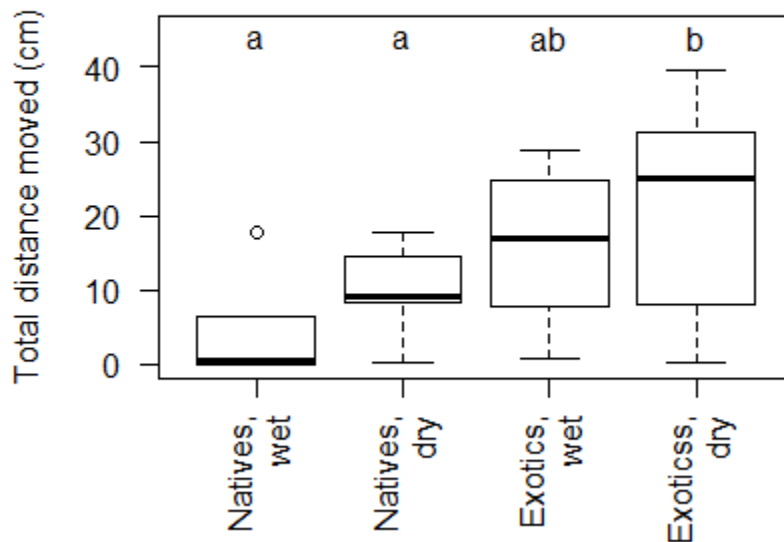
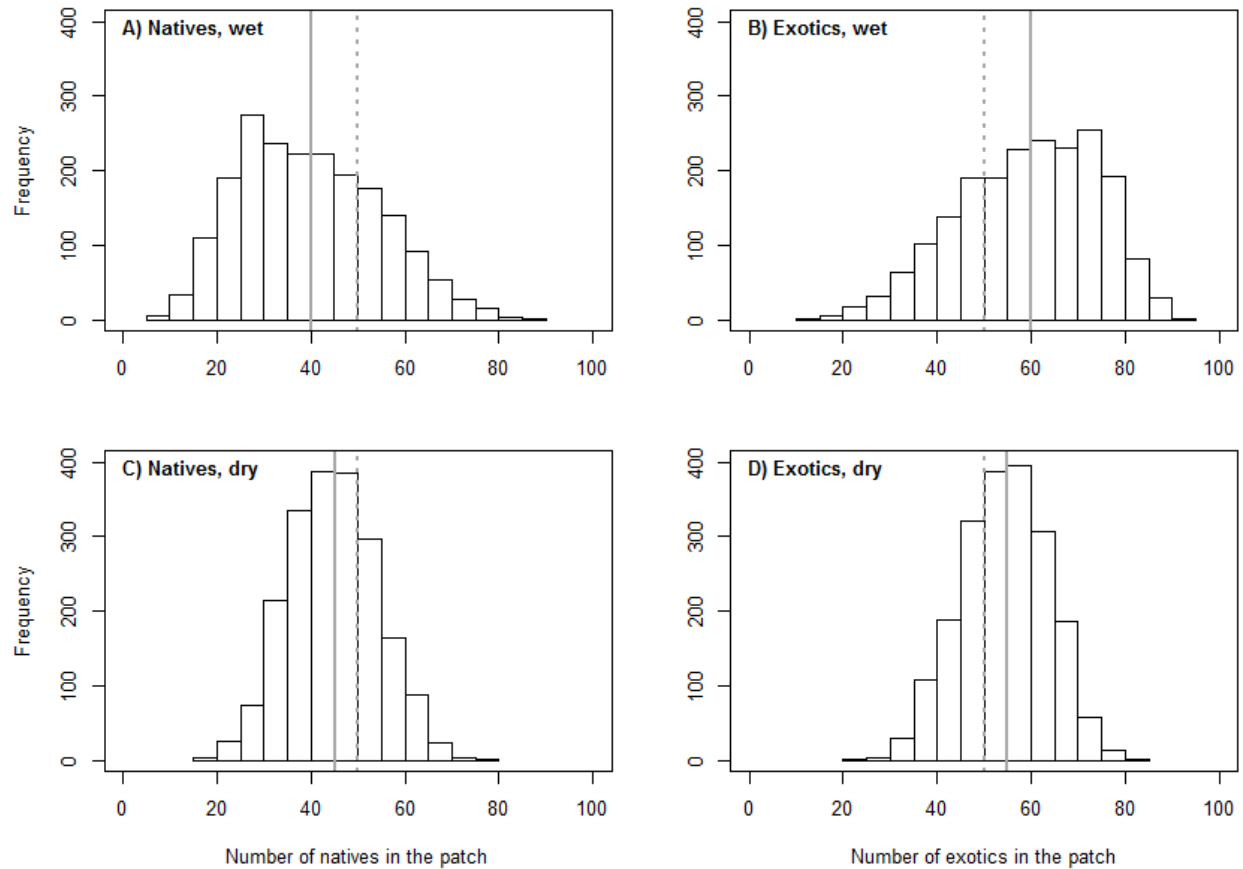


Figure 2. Histograms of number of natives in each patch at the end of the simulation, with data from all 100 replicates of the simulation pooled, for a total of 2000 patches represented. The dotted vertical line indicates abundances of 50, where patches have equal amounts of native and nonnative snails. The solid vertical line is the mean of the distribution.



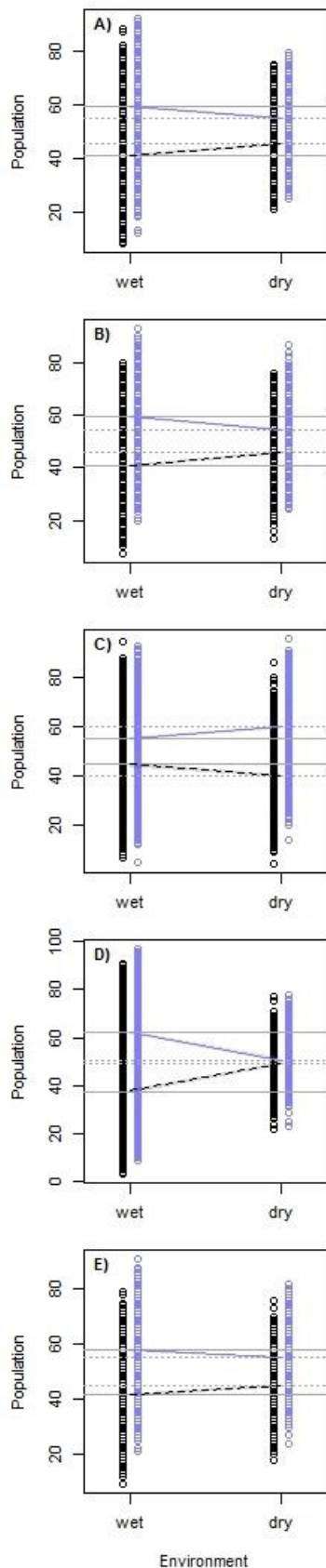


Figure 3. Abundances of native and exotic snails in wet and dry environments. Each point represents a single patch. Black points are exotic snail abundances and blue (grey) points are native snail abundances. The dashed black line represents the difference in abundance in native snails between wet and dry environments. The blue (grey) solid thick line represents the difference in abundance in exotic snails between wet and dry environments. Both sloped lines in each plot are derived by sampling from the MCMC model fit to the data. The pairs of solid, grey, horizontal lines represent the mean population abundance in wet environments. The dotted, grey, horizontal lines represent the mean population abundance in dry environments. The higher line in this pair is the abundance of exotics and the lower line is the abundance of natives. Simulations in each plot consisted of data A) based on the relative movement rates in each treatment, B) in the same proportion as A, but shifted up, C) with a large difference between native and nonnative movement rates in dry environment, D) with a large difference between native and nonnative movement rates in wet environment and E) with a difference between native and nonnative movement rates is equal in both environments.