The Resilience of a Swarm Ecosystem Under Environmental Variation

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Abstract

Evolving swarms can be used both to solve real-world problems and to study biological and ecological phenomena. We simulated an evolving swarm of birds under three different types of climate-change-related environmental variation - a temperate environment becoming tropical, a temperate enviroment becoming a desert, and a tropical environment becoming a desert. We found that desertification increased expirations within the swarm and decreased population stability. The direction of the variation - tropicalification or desertification - had a greater impact on the dynamics of the swarm than the degree of variation when it came to these outcomes. The environmental variation also affected the genetics of the birds, with decreased food availability leading to collision avoidance genes being downplayed, and searching behavior for food being changed. High-intensity environmental variation led to less genetic stability post-change than lower-intensity environmental variation.

Swarming and flocking behavior is ubiquitous throughout all scales of biological and physical systems. Swarming simulations were first developed by Reynolds (1987) using his boids, simple agents that moved according to a set of basic rules. Much later swarming behavior simulation work has focused on agent-based modeling, which is centered around the modeling of populations of individuals with rules governing their behavior (Mach and Schweitzer, 2003). Agent-based modeling has been used to study such subjects as the dynamics of mountian pine beetle infestations of forests (Perez and Dragicevic, 2010) and the dynamics of how bacteria aggregate to form microfilms (Lardon et al., 2011). Recent advances in robotics have made it possible to experiment with large-scale physical swarms of robots (Rubenstein et al., 2012).

Swarm flying behavior is increasingly an area of interest, with a variety of algorithms and applications being developed. Karaboga (2005) used simulations of bee swarm flying to develop a numerical optimization method, and Su et al. (2009) modeled flocking behavior in the presence of a group leader. Optimization of heterogenous swarms of flying agents is challenging, but is potentially very useful in applications such as crop polination (Nagpal et al., 2011; Berman et al., 2011). Flying swarms have also been applied in the lab to tasks such as chemical cloud detection (Kovacina et al., 2002) and dynamic communications relays (Hauert et al., 2008).

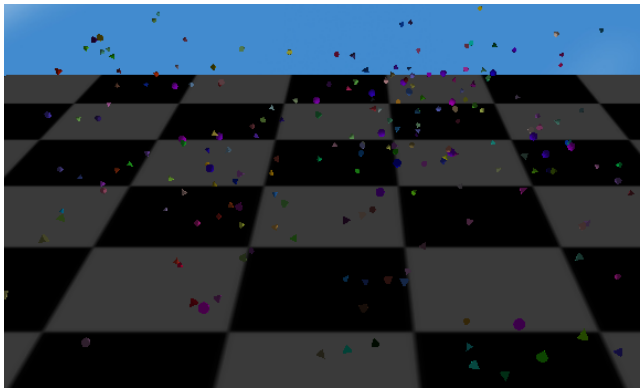


Figure 1: Example of evolving swarm and environment.

Evolving Swarms

One major concern of evolutionary biology, which has been studied by both biologists and computer scientists, is the evolution of collective behavior (such as group foraging and swimming in schools) among a group of organisms. Previous studies have examined the evolutionary risks and benefits of some of these behaviors, and have examined them as optimization processes that could be stable or unstable under different circumstances (Davies et al., 2012; Pulliam and Caraco, 1984; Sibly, 1983). Artificial life researchers have used computational systems to study the evolution of parasitism (Ray, 1991), the collective behavior of flying and swimming organisms (Reynolds, 1993; Zaera et al., 1996), and the interactions of evolution and game theory (Eriksson and Lindgren, 2002).

In recent years there has been some success in evolving collective behavior amongst flying artifical agents using SwarmEvolve and SwarmEvolve 2.0 Spector and Klein (2002); Spector et al. (2005), which modeled 3D virtual worlds and allowed for goal orientation, multiple species of

birds, and evolution of the motion control equation itself. This success has been followed by other work in evolving coordinated flying groups (Knoester and McKinley, 2011) as well as evolving other kinds of group behavior such as wolf-pack hunting (Muro et al., 2011).

Evolution and Environmental Variation

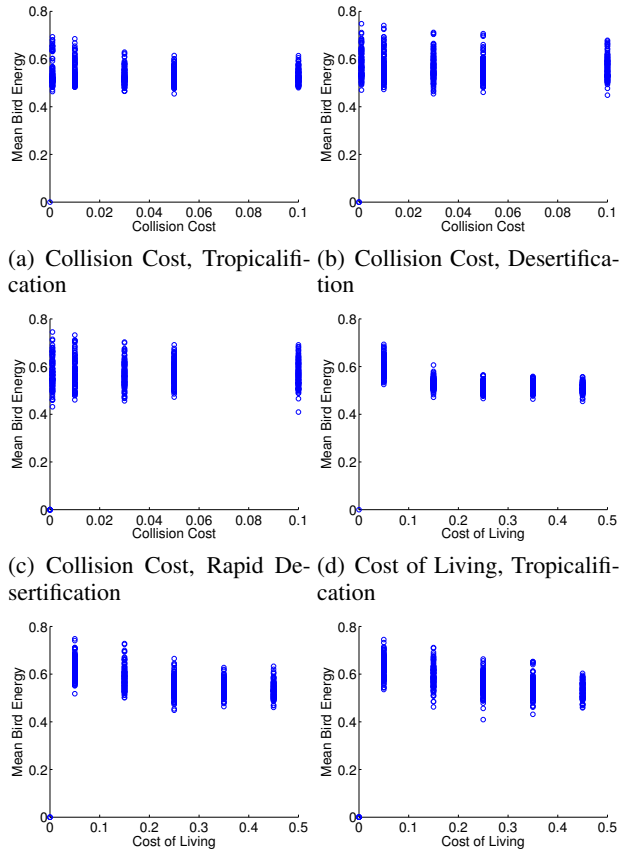
In the study of evolution and ecology, environmental variation is receiving increasing attention as a factor due to concerns about climate change. Ruel and Ayres (1999) used Jensen's inequality, a mathematical proof, to predict some effects of environmental variation on biological systems. Other studies have found that environmental variation affects the ability of species to coexist (Chesson, 1986) and that the more abrupt environmental variation of climate change has different effects on population dynamics than does natural environmental variation (Ruokolainen et al., 2009). In microbial ecosystems, the resilience of populations has been linked to the degree of environmental variation, where harsh variations can trigger population collapse (Sanchez and Gore, 2013). Several researchers (Visser and Both, 2005; Stenseth and Mysterud, 2002) have studied the potential effects of climate change on periodic animal and plant life cycle events, and the effects of such mistiming on food availability (Both, 2010). Recently, evolutionary game theory (Weibull, 1997) has been applied to questions of environmental variation, climate change, and ecology (Johansson and Jonzén, 2012a,b).

In this paper, we examine the effects of different forms of environmental variation on the evolution of a flying swarm.

Model

Simulation is performed with the Brevis simulator (Harrington, 2014), a scientific and artificial life simulator. Brevis provides simulation and visualization capabilities via the Java JVM and the programming language, Clojure. In addition to visualization, Brevis provides a number of simulation features including neighborhood and collision detection, both of which are key to 3D swarm simulations.

Our model consists of a population of birds with 6 continuous genetic traits and a set of foods (energy sources). The flight of a bird is controlled by its genes, similarly to (Reynolds, 1987). Each bird uses the first bird and first food in its list of neighbors, if there are any neighbors of either type within the neighborhood radius (10,000 units, in this case). The direction vectors between the bird and its neighboring food and bird are then computed. If the respective entity does not exist in the neighborhood a vector of magnitude 0 is used. While we have chosen to use a neighborhood size that is large enough to ensure that birds will always have another bird and food in its neighborhood, alternative default behaviors may be more favorable. The direction vectors are then weighted based upon whether the distance between the bird and the entity is "close" or "far,"



(a) Collision Cost, Tropicalification

(b) Collision Cost, Desertification

(c) Collision Cost, Rapid Desertification

(d) Cost of Living, Tropicalification

(e) Cost of Living, Desertification

(f) Cost of Living, Rapid Desertification

Figure 2: Collision cost (a-c) and cost of living (d-f) vs mean bird energy in tropicalification, desertification, and rapid desertification simulations, with best-fit quadratic curves displayed.

where 2 distance genes determine this threshold for neighboring birds and foods. The sum of the weighted vectors is then taken as the bird's new acceleration vector. A planar floor is positioned in the world at y = 0, and when birds collide with the floor they "land," such that they lose their current velocity and acceleration, reorient to be perpendicular to the floor, and automatically push off with small initial velocity and acceleration.

Energy

Energy is the currency of our simulation. Birds require energy to live, and foods produce energy over time. Each bird is subject to a constant cost of living, which influences how long a bird can survive between feedings. The energy in foods are replenished a constant rate (0.1 units/timestep). Energy is transferred between entities when collisions occur. A collision between two birds results in an energy loss for both birds. Collisions between a bird and a food result in a transfer of energy from the food to the bird at a rate of

0.005 units/timestep. When a food's energy reaches zero, it is removed from the simulation and replaced by a newly initialized and randomly positioned food. If a bird's energy reaches zero, it is removed by the simulation and replaced. In our experiments we study a range of values for both the cost of living for birds, and the cost of collisions between birds.

Evolution

Each bird has a genome of 6 genes, which is used to control its flight acceleration. Two genes are distance thresholds that indicate whether an entity is considered close or far, for neighboring foods and neighboring birds. The remaining 4 genes are coefficients that specify the weights for the close/far neighboring birds/foods. Distance threshold genes are bounded by the hypotenuse of the area containing food (565.69 units), while the remaining acceleration weighting genes are within $[-10, 10]$. By using a fixed set of continuous traits, the genetic diversity in the population is mostly regulated by selection dynamics, whereas genetic diversity in models utilizing discrete traits is more vulnerable to loss of diversity via mutation.

Every time a bird runs out of energy, it is replaced. The replacement is the mutant of a randomly selected living bird that has been alive for more than 1 timestep 99% of the time, and 1% of the time a completely randomly generated bird is used as the replacement. Mutation is achieved by adding/subtracting random values to each gene in the mutant. Birds better able to survive implicitly have more opportunities to reproduce.

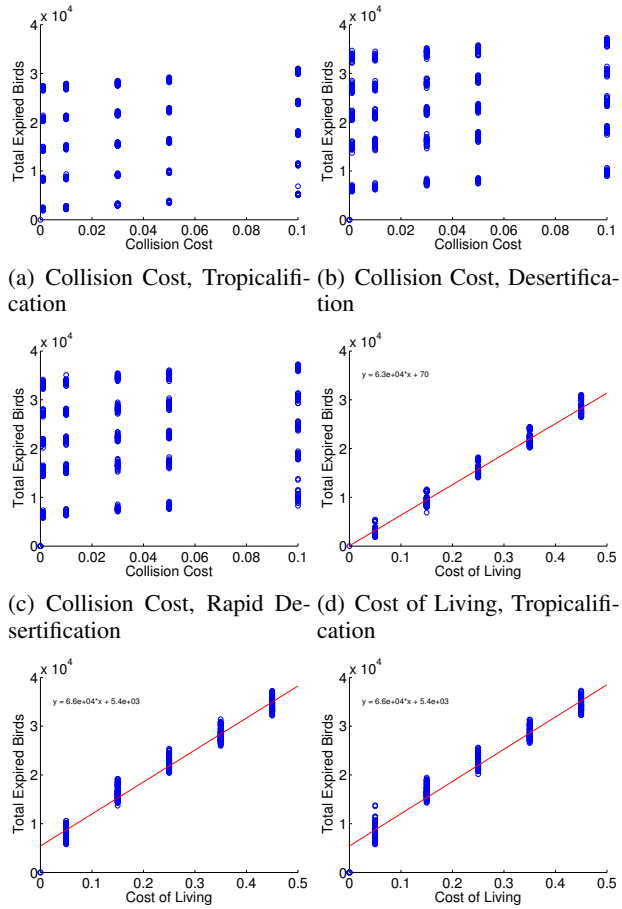
Experiments

We ran simulations of 250 birds each over 100,000 timesteps[1]. In each simulation, the birds randomly traversed a world containing scattered food items, where a bird gains energy from colliding with a food item. Birds were required to maintain a certain level of energy in order to survive, and could expire either from insufficient energy or from exceeding a maximum lifespan, with any expired bird being replaced by a new bird.

Different environments were represented by different food densities. The "uniform-high" environment, representing a tropical or other lush climate, was characterized by a uniformly high food density. The "uniform-low" environment, representing a sparsely-vegetated climate such as a desert or tundra, was characterized by a uniformly low food density. The "seasonal" environment, representing a temperate climate, had "summers" of high food density and "winters" of low food density.

Each simulation switched from one environment to another at the halfway point, with three types of environmental variation being tested. The first two types, uniform-high to uniform-low and seasonal to uniform-low, represent desertification of tropical and temperate environments, respectively. The third type, seasonal to uniform-high, represents the encroaching of tropical climates onto previously-temperate environments. We refer to these as "tropicalification," "desertification", and "rapid desertification."

For each type of environmental variation, we sampled across different values for two parameters, meant to approximate certain real-world ecosystem dynamics. The first, collision cost, takes away a certain amount of energy from a bird that collides with another bird, and is meant to approximate the effects of competition. The second, cost of living, is the amount of energy that a bird must take in over a certain time period in order to stay alive. Simulations for all three types of environmental variation were run with collision costs of 0.001, 0.01, 0.03, 0.05, and 0.1, and costs



(a) Collision Cost, Tropicalification

(b) Collision Cost, Desertification

(c) Collision Cost, Rapid Desertification

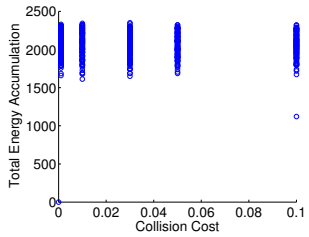
(d) Cost of Living, Tropicalification

(e) Cost of Living, Desertification

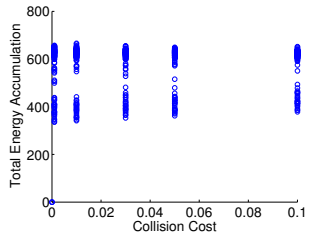
(f) Cost of Living, Rapid Desertification

Figure 3: Collision cost (a-c) and cost of living (d-f) vs total expired birds in tropicalification, desertification, and rapid desertification simulations, with best-fit lines displayed for d-f.

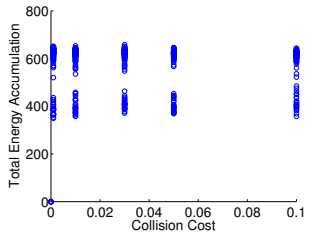
[1]Simulation code used for this study will be made publicly accessible upon completed documentation via the Brevis website: http://brevis.golemics.org



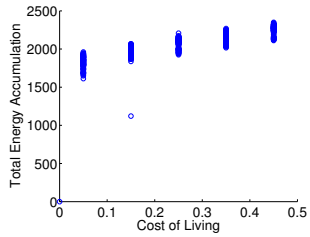
(a) Collision Cost, Tropicalification



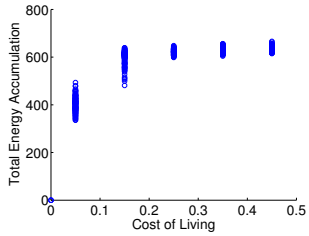
(b) Collision Cost, Desertification



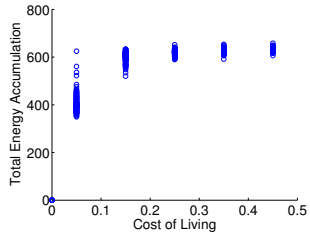
(c) Collision Cost, Rapid Desertification



(d) Cost of Living, Tropicalification



(e) Cost of Living, Desertifiation



(f) Cost of Living, Rapid Desertification

Figure 4: Collision cost (a-c) and cost of living (d-f) vs total accumulated energy in tropicalification, desertification, and rapid desertification simulations, with best-fit quadratic curves displayed for d-f.

of living of 0.05, 0.15, 0.25, 0.35, and 0.45. Each set of collision cost and cost of living parameters was used in 25 simulations.

Results and Discussion

We look at how our two parameters that mimic ecological dynamics, collision cost and cost of living, are associated with three different variables - mean bird energy, total expired birds during the last quarter of the simulation, and total accumulated energy during the last quarter of the simulation. We measured mean bird energy three quarters of the way through each simulation, so that we would see their values midway through the post-environmental-change period, once the birds had had some chance to adapt to the new environment. Total expired birds and total accumulated energy were measured for the last quarter of each simulation, so that the measurements would start after the birds had had the opportunity to adapt to the new environment and so that there would be enough time remaining for a cumulative metric to be reasonable.

We first looked at how collision cost and cost of living are associated with mean bird energy. In Fig.2(a)-2(c), we can see how collision cost is associated with mean bird energy for all three types of environmental variations. The differences between tropicalification, desertification, and rapid desertification here are very subtle. Both types of desertification showed slightly wider ranges of mean bird energy across simulations with the same collision cost. However, increasing collision cost had minimal effect on mean bird energy.

The effect of cost of living on mean bird energy, shown in Fig. 2(d)-2(f), depended on what sort of environmental variation took place in the simulation. As with collision cost, both forms of desertification produced wider ranges of results for the same cost of living, suggesting that desertification causes more unpredictability regarding mean bird energy than tropicalification. In all simulations, mean bird energy fell as cost of living increased and birds needed to expend more energy in order to survive. However, in the tropicalification simulations, the decline in mean bird energy gradually leveled off as cost of living increased, while in both types of desertification simulations, this leveling off was less clear. This suggests that the birds may have been more resilient to increased energy needs when food became more plentiful rather than more scarce.

Next, we looked at how collision cost and cost of living influenced the total number of expired birds in the simulations. In both cases, the type of environmental variation - tropicalification vs desertification - made the biggest difference, with desertification of any kind leading to more expired birds.

When collision cost was correlated with total expired birds, as shown in Fig. 3(a)-3(c), we found that there was a small increase of expired birds as collision cost increased, and this was true for both tropicalification and desertification simulations. This is an intuitive result, as the steeper sudden drops in a bird's energy caused by higher collision cost would make it more likely to fall under the energy threshold needed for it to stay alive. Desertification situations, in which once-plentiful food became more scarce, also unsurprisingly led to more expired birds than the reverse situation. In the desertification simulations, the number of expired birds at the same collision cost was not only slightly higher but also more *variable* than in the tropicalification simulations, and rapid desertification was correlated with slightly more variability than slow desertification. If we recall that collision cost is meant to approximate competition for territory between birds, this result makes sense. As food becomes more sparsely distributed, more birds will need to feed from the same areas of the map. There is a tradeoff between being able to find food and being able to avoid collisions. In different simulations this tradeoff may play out with slightly different dynamics, leading to greater variabil-

ity. Since the change in food geography is more drastic in rapid than in regular desertification, the effect is greater in rapid desertification. Total expired birds over different experimental runs could be grouped into five clusters, which correspond to the different costs of living in different runs, suggesting that cost of living plays a greater role in bird expirations than collision cost.

As with the previous figure, in Fig. 3(d)-3(f), we see that desertification of any sort increases the overall number of expired birds. Under all three types of environmental variance, we see that increases in the energy needed to live lead to increases in the number of expired birds, as the birds have a more difficult time maintaining the higher levels of energy. We also see that in the desertification simulations, the rate at which expired birds increase with cost of living increases, which can clearly be seen with the increased slopes ($P = 0.032$ and $P = 0.036$) of the best-fit lines in the desertification graphs as compared to the tropicalification graph. However, there is little difference between the two types of desertification - going from a high-energy environment to a low-energy one seems to be just as much of a problem in this case as going from a seasonal, temperate environment to a low-energy one.

Finally, we looked at how our varying parameters influenced the total accumulated energy in the simulations. Unsurprisingly, it was much higher overall - by more than a factor of three - in the tropicalification simulations where food started out adequate and became plentiful, regardless of these parameters. In Fig. 4(a)-4(c), we can see that collision cost had little influence on total accumulated energy, but desertification was connected to bimodal levels of total accumulated energy at low and moderate collision costs, with some simulations accumulating a high level, and some at the same collision cost accumulating a low level. This may be an indication that sometimes, under these collision costs, the birds were able to evolve reasonably quickly to be able to find the sparser food, and sometimes they were not. Again, there is a potential tradeoff between being able to find the food and being able to avoid collisions, as the same number of birds feeds from fewer food sources. The observed bimodality was less strong with the regular desertification than with the rapid desertification, indicating a gradual slide into bimodality as the intensity of environmental variation increases.

In Fig. 4(d)-4(f), the plots of the two different types of desertification simulations against energy cost of living are similar to each other, but under rapid desertification, there was slightly more variance ($P = 0.0013$) in total accumulated energy, especially at low cost of living. This may be because of the greater instability in the system introduced by the more rapid change.

Overall, desertification vs tropicalification had a greater impact than degree of desertification across the board, with the results from the two different types of desertification being very similar.

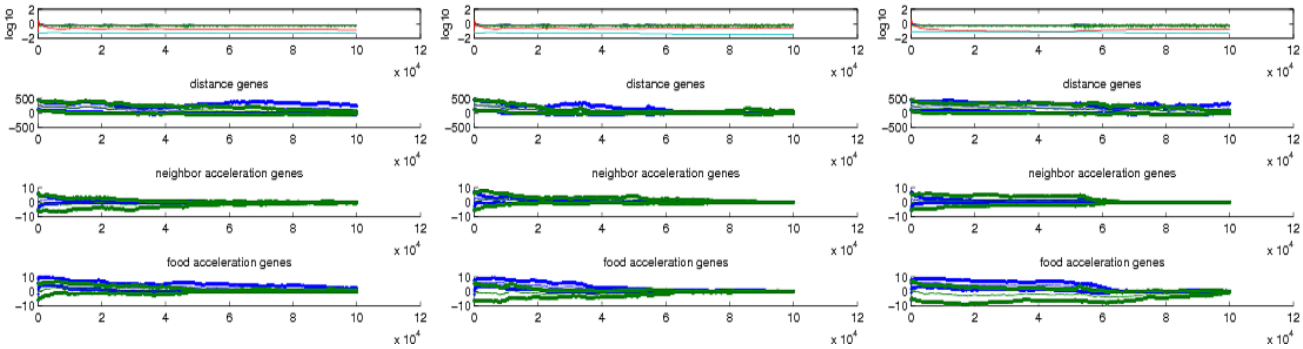
Evolution of Genes

We also tracked the effects of environmental variation on our swarms at the genetic level. This is depicted for three simulations, one of each environmental variation type, in Figs. 5(a)-5(c). Each bird has 6 evolving genes to control flight acceleration, which are described in more detail in the "Model" section above. The distance genes neighborD and foodD set the thresholds for how close a neighboring bird or food source, respectively, has to be to the bird to be considered "close" vs "far." The other four genes specify weights for close/far neighboring birds and foods. In this way, neighbor acceleration genes (neighborC and neighborF) assist in collision avoidance while food acceleration genes (foodC and foodF) assist in finding food.

Under conditions of rapid desertification (with the environmental variation taking place halfway through, as in all the simulations), the weights of neighbor acceleration genes go quickly to zero or near zero, flatlining by the time the simulation is 70% complete. Under regular desertification this process is slower, not completing until more than 80% of the way through the simulation, and under tropicalification it does not quite happen at all. This suggests that a switch from a more food-rich to a food-scarce environment particularly selects for birds that seek out neighbors rather than avoiding them, as the presence of other birds can mean the presence of food, but it also suggests that this is a useful trait in general (particularly at such a low collision cost), as the magnitudes of weights of the neighbor acceleration genes decreased significantly even in tropicalification.

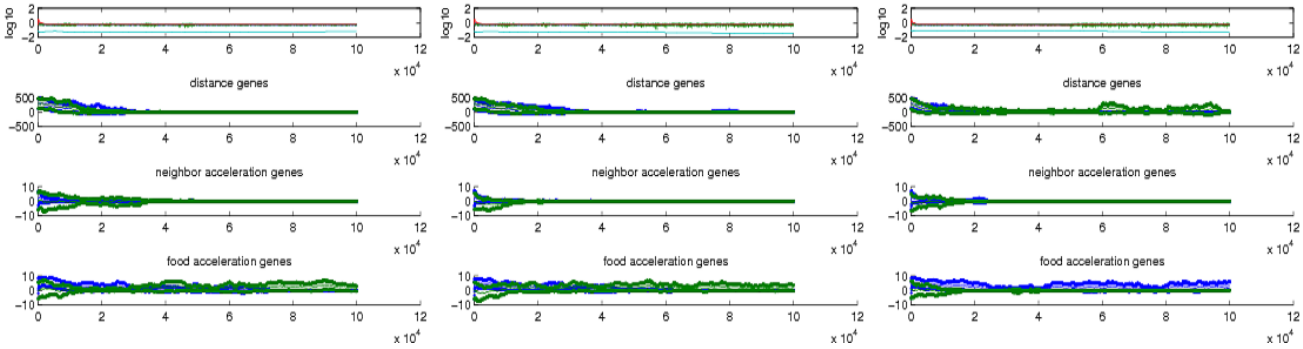
In the tropicalification simulation, the thresholds for considering a neighboring bird "close" as set by neighbor distance genes increased over time, while those of food distance genes decreased. This was not true in either of the desertification simulations - while the distance thresholds fluctuated after rapid desertification, apparently unable to stabilize after the shock to the system, their averages over time stayed nearly level, and during regular desertification it was the food distance thresholds that gradually increased. The fact that food was easier to find in the "tropics" may have meant that there was no need for relatively faraway foods to be considered "close" and easily detectable for birds, while with neighbors more spead out rather than flocking to the same food sources, there was evolutionary selection pressure to be able to detect and avoid colliding with less-predictably-located neighbors. In desertification the reverse pressure would naturally be exerted for food, though it is is interesting that in the more intense desertification situation, in which the birds were adjusting to a larger change, they were unable to evolve this threshold pattern over the time given by the simulation.

Unsurprisingly since our modeling of environmental variation centered around food availability, food acceleration



(a) Tropicalification (b) Desertification (c) Rapid Desertification

Figure 5: CoL = 0.05, CC = 0.001. In the top subplots, blue is the mean energy per bird, green is the mean energy per food, red is the bird expiration rate, and turquoise is the mean accumulated energy per bird. In the distance genes suplots, blue represents the neighborD gene and green the foodD gene +/- a standard deviation. In the neighbor acceleration genes subplots, blue represents neighborC, and green, neighborF, +/- a standard deviation. In the food acceleration genes subplots, blue represents foodC, and green, foodF, +/- a standard deviation.



(a) Tropicalification (b) Desertification (c) Rapid Desertification

Figure 6: CoL = 0.15, CC = 0.15. In the top subplots, blue is the mean energy per bird, green is the mean energy per food, red is the bird expiration rate, and turquoise is the mean accumulated energy per bird. In the distance genes suplots, blue represents the neighborD gene and green the foodD gene +/- a standard deviation. In the neighbor acceleration genes subplots, blue represents neighborC, and green, neighborF, +/- a standard deviation. In the food acceleration genes subplots, blue represents foodC, and green, foodF, +/- a standard deviation.

genes were notably influenced by type of environmental variation. Under regular desertification, the weight magnitudes of the foodF genes go nearly to zero, and there is some slight maintenance of the weight magnitudes of the foodC ones. Under rapid desertification, all food acceleration genes had high (though gradually decreasing) weight magnitudes when food was plentiful, but those of foodC genes go nearly to zero while those of foodF genes maintain better - the opposite of the tropicalification simulation, in which the weight magnitudes of foodF genes go nearly to zero while those of foodC genes maintain better. This makes sense, as in the former case, food is more likely to be far away from any given point in the world, while in the latter, food is likely to be nearby and there is less need to be able to deal productively with faraway food.

For comparison, we look at the results of simulations with a higher collision cost and cost of living (both 0.15), which are visible in Figs. 6(a)-6(c). In these, we see the weight magnitudes of neighbor acceleration genes neighborC and neighborF going nearly to zero in all three simulations even before the environmental variation - even with the strongly increased collision cost, the increased cost of living appears to make finding food more important than being able to avoid neighbors. Distance genes foodD and neighborD, whose thresholds go to zero in the other simulations, fluctuate after rapid desertification, especially foodD - while in the slower cases, the birds are adapting relatively quickly to new needs around food, the larger perturbation of food availability in the rapid desertification scenario appars to make these genetics unstable, as also happened with lower collision cost

and cost of living.

The food acceleration genes show an intriguing pattern - in both simulations where the environment starts out seasonal, the weight magnitudes of the foodF genes quickly increase (and do so further after the environmental change), but in the rapid desertification simulation the foodC genes start out with higher weight magnitudes that start to decrease before increasing again but fluctuating after desertifiction. One might assume that this is because the rapid desertification scenario is the only one in which food started out at its most plentiful, making it less necessary to need to seek out faraway food and more necessary to seek out close food, however, this does not explain why this was still the case after desertification. Once again, as with the distance genes in the same scenario, the rapid, intense environmental variation is connected with a lack of genetic stability that is not seen with the other forms of environmental variation. Indeed, the post-change lack of genetic stability in the population seems to be a characteristic of the rapid desertification scenario at these moderate collision cost and cost of living parameters, and is even seen to a lesser extent using the more survival-friendly parameters discussed previously. In all cases food acceleration genes play a much greater role than when cost of living was lower.

We have simulated a swarm of birds evolving genetically and behaviorally to three different types of environmental variation, meant to approximate types of variation seen in the real world during times of climate change - a temperate seasonal environment to a tropical one, a seasonal enviroment to a desert, and a tropical environment to a desert. We found that desertification in particular led to negative outcomes such as increased expired birds and decreased population stability (as indicated by the amount of variation on such metrics as mean bird energy or total accumulated energy between simulations that used the same parameters). The direction of the variation - tropicalification or desertification - had a greater impact on these outcomes than the intensity of the variation (seasonal to desert vs tropical to desert). The environmental variation also affected the genetics of the birds, with decreased food availability leading to selection against collision avoidance genes, and food availability influencing whether bird ability to find nearby food or faraway food was favored. A greater intensity of environmental variation led to less stability in population genetics post-environmental shift. In the wake of concerns about climate change, it is increasingly important to be able to predict how populations will fare under environmental variation. As Sanchez and Gore (2013) found that harsher environmental variation led to decreased resilience in microbial populations, we have found that it led to decreased genetic resilence in our simulated birds. In addition, we have identified the type rather than just the intensity of variation as another factor influencing resilience.

Acknowledgements

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