

Dispatches

Evolutionary Ecology: Old Ideas Percolate into Ecology

A novel model derived from percolation theory suggests that phase polyphenism may have initially evolved in locusts as a behavioural strategy to reduce the connectivity between patches of vulnerable prey, so reducing predation risk.

Kenneth Wilson

In 1982, Kenneth G. Wilson (no relation) won the Nobel Prize for Physics in recognition of his research applying a mathematical tool he borrowed from quantum field theory, known as the renormalization group, to problems in statistical physics, including phase transitions [1]. One of the areas to benefit from this approach was 'percolation theory' — the study of how randomly generated clusters connect and behave (the name is derived from the way in which coffee flows through a percolator). Now, more than a quarter of a century later, population ecologists are beginning to borrow the same modelling framework to address problems in ecology and evolution. The latest of these is reported in this issue of *Current Biology*, in which Reynolds and colleagues [2] discuss how percolation theory might help to explain the evolution of phase polyphenism in locusts.

Phase polyphenism is a phenomenon most commonly observed in insects and occurs when cues associated with population density trigger individuals to switch between two phenotypes — one adapted to low population densities and the other adapted to high densities [3]. This phase transformation is associated with changes in morphology, physiology and behaviour [3,4]. In desert locusts, nymphs of the low-density *solitaria* phenotype are green, cryptic and reclusive in nature, whereas the high-density *gregaria* form is aposematic yellow-and-black and highly gregarious, actively seeking out other locusts (Figure 1). Phase polyphenism in locusts has intrigued biologists for decades [4], and Reynolds *et al.* [2] use percolation theory to suggest a novel mechanism to explain its evolution.

So, what is percolation theory? This question is best addressed by way of an example [5]. Imagine two villages

separated by a forest of trees (Figure 2). A spark from a bonfire in one of the villages spills into the forest and a tree catches fire. What is the probability that the fire will spread to set alight the village on the other side of the forest? Clearly, the fire can spread from tree to tree and, if the trees are close enough together that every burning tree will ignite one or more of its neighbours, then the fire will spread rapidly between the two villages. However, if clusters of adjacent trees are sufficiently far apart that burning trees cannot set alight their closest neighbours, then the fire will eventually go out and the second village will be saved; this is the rationale for fire-breaks.

In percolation theory, the forest in this example is approximated as a lattice in which squares are either occupied by a tree, with probability p , or are empty, with probability $(1 - p)$. If all of the squares are occupied by trees, as might be the case for an intensively managed plantation, then $p = 1$ and the fire will always spread rapidly between

the two villages. But if there are gaps in the forest then $p < 1$, and the probability that the fire will spread from one village to the other is determined by the exact proportion of squares occupied by trees. Specifically, if the proportion of occupied squares is less than some critical threshold, known as the *percolation threshold*, p_c , then the fire will always go out before crossing the forest, whereas if it is greater than this threshold ($p > p_c$), then the fire will always spread between the two villages. The average time before the fire goes out then depends on the value of p relative to p_c . For p near to one, the wave of fire quickly sweeps across the lattice of trees and the fire is rapidly extinguished, leaving behind the charred remains of the forest (Figure 2D). For p near zero, most burning trees have no neighbours and so the fire quickly stops after clusters of burning trees fail to ignite their distant neighbours (Figure 2F). As p approaches p_c , a path of neighbouring trees will gradually emerge, which eventually connects the two villages when $p = p_c$; it is at this point that the fire burns the longest, as it snakes through the forest from tree to tree (Figure 2E).



Figure 1. Phase polyphenism in action: *solitaria* (left) and *gregaria* (right) phenotype of the desert locust, *Schistocerca gregaria*.

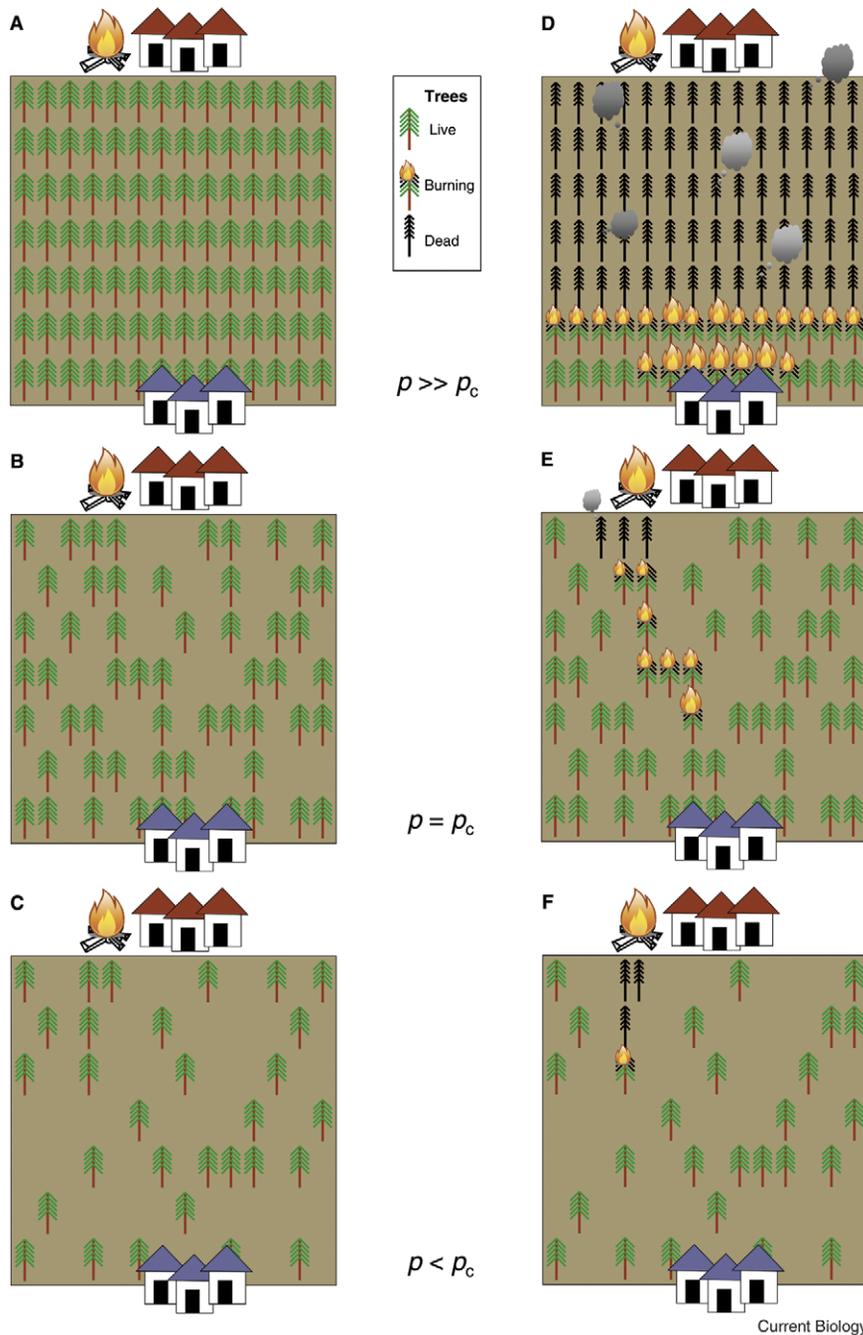


Figure 2. Percolation theory applied to forest fires.

Panels (A–C) show the spatial distribution of trees in a forest separating two villages; panels (D–F) show how this influences the spread of a fire through the forest starting near the top village. In (A) the density of trees is very high, such that each tree is adjacent to another tree and there are no gaps: that is, $p \gg p_c$, where p is the proportion of sites (or matrix squares) filled by trees, and p_c is the percolation threshold, see main text. As a result, the fire spreads rapidly from one village to the other (D). In (B), the density of trees is much lower, but the proportion of occupied sites is high enough for there to be a chain of trees connecting the two villages together ($p = p_c$), such that a fire in one village can slowly spread from tree to tree, eventually setting alight the other village (E). In (C), the density of trees is lower than the percolation threshold ($p < p_c$), and so when a fire from one of the villages ignites trees on the edge of the forest, it quickly burns out because there are no adjacent trees for the fire to ignite (F). Reynolds *et al.* [2] use an analogous use of percolation theory to explain the evolution of phase polyphenism in locusts, with locusts replacing the trees and predators replacing the fire.

How can models of forest fires help explain the evolution of phase polyphenism in locusts? First, imagine a population of locusts in a landscape (or lattice), much like the trees in our forest. If individuals behave randomly with respect to each other, then as population density increases so the average distance between locusts will decrease and clusters of locusts will form. Ground-foraging predators, such as lizards and small mammals, will feed on locusts, as will more mobile predators like birds [4]. When the predator has finished eating a particular locust, or has depleted a cluster of locusts below the density that makes it uneconomical for it to stay any longer, then the predator may simply move through the landscape in search of more locusts to feed on. If the locust population density is high enough, then our predator will be able to easily move through the landscape from cluster to cluster, just as the fire spreads rapidly through our densely-planted forest. But if the locust population is too small, then the nearest locust(s) may be too far away to be worth pursuing and the optimal behaviour for the predator may be to switch to a different prey species, breaking the chain of predation (analogous to our fire burning itself out).

Thus, as with the forest fire scenario, there will be some critical threshold for percolation, p_c , above which foraging on connected clusters of locusts is sustainable and the predator's optimal behaviour is to specialise in feeding on locusts, and below which it is unsustainable and the predator should switch to feeding on other prey species. So, how does this help explain why locusts exhibit phase polyphenism? Reynolds *et al.* [2] use percolation theory to argue that, in these circumstances, when population density exceeds the critical threshold, p_c , it pays the locusts to 'flip' from a dispersed solitary state to instead form tight cohesive groups. This is because by doing so they reduce the number of connections between clusters to a value below the threshold allowing sustainable predation. In other words, if population density is high enough that randomly distributed locusts would form a connected network of clusters in the landscape, then by coalescing into larger, but more dispersed groups, they reduce the relative connectivity of those locust

clusters, reducing it below the threshold for percolation.

Although some of the ideas in this paper have clear parallels with those in Turner's and Pitcher's [6] 'attack abatement' model, the notion of a critical *percolation threshold* triggering gregarious behaviour is entirely novel. The Reynolds *et al.* [2] paper is important for a number of other reasons. For one thing, this is the first time that percolation theory has been used to understand the benefits of group-living as an anti-predator defence. Indeed, although percolation theory is commonly used in physics, materials science, engineering and chemistry, less than 3% of the 1000+ papers published in this area over the last five years have addressed ecological or environmental issues (ISI Web of Knowledge).

Secondly, the paper illustrates how percolation theory might be applied more generally to understand the evolution of group-living [7]. Previous studies have argued that living in groups may have evolved as a defence against parasites and pathogens, because by aggregating together the connectivity between groups of potential hosts is reduced and there is an increased probability that disease epidemics sweeping through a population will fade out, because of a shortage of nearby susceptible hosts [8]. Whilst spatially-explicit agent-based models seem to confirm the benefits of group-living as

an anti-parasite defence, percolation theory has not yet been applied in this context (but see [9]). However, it seems likely that percolation theory may provide a general theoretical framework for understanding the evolution of gregarious behaviour as a defence against any natural enemy that exploits clusters of hosts.

Thirdly, this study is important because it suggests that aggregative behaviour may have been the first step in the evolution of the suite of traits we commonly refer to as phase polyphenism. This is because it argues that there are benefits to individuals of congregating in groups even in the absence of any benefits associated with unpalatability, aposematic coloration or kin-selection. Once gregarious behaviour has evolved, selection would then favour other traits to maximise the benefits of group living and to minimise its costs, including the evolution of aposematism [10], cannibalism [11], and density-dependent prophylaxis [12]. Whilst a spatially-explicit evolutionary model has yet to be developed to explore these ideas fully, it seems likely that the use of percolation theory to study the evolution of aggregative behaviour will prove to be a highly significant advance. Hopefully, percolation theory will permeate further into mainstream evolutionary ecology than it has done since its origins more than a quarter of a century ago.

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Perceptual Learning: Inverting the Size–Weight Illusion

When one lifts two objects of equal weight and appearance but different size, the smaller object usually feels heavier. New results show that this size–weight illusion can be inverted after extensive training with objects in which the natural size–weight relationship is artificially reversed.

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The size–weight illusion, whereby a smaller object feels heavier than a larger one of equal weight, was first described over 100 years ago by Charpentier ([1]; see [2]). In the natural environment, an object's weight is positively correlated with its size. Thus when one lifts the larger of two objects,

it is expected to be heavier. According to most hypotheses, the size–weight illusion occurs when this expectation is not met. In particular, it has been argued that the illusion might be caused by a mismatch between the sensorimotor prediction and the actual weight. According to this mismatch hypothesis, the wrong prediction would lead to motor commands

scaled inappropriately for the object's weight. A few years ago, Flanagan *et al.* [3] disproved this hypothesis by showing that, after repeated lifting of the same objects, the sensorimotor prediction adjusts such that the load-force when grasping the objects is scaled correctly, while the size–weight illusion persisted. If not a sensorimotor mismatch, perhaps a perceptual mismatch causes the illusion, or is the illusion even independent of prior expectations?

In a recent paper in *Current Biology*, Flanagan *et al.* [4] report that the size–weight illusion can be inverted after extensive training with objects in which the size–weight relationship is artificially reversed. They also show