AN APPLIED CASE STUDY of the complexity of ecological systems and process: Why has Lyme disease become an epidemic in the northeastern U.S. over the last few decades? Where did it come from? What causes Lyme disease?
Frequency of DIAGNOSED Lyme disease cases have increased several-fold in the last couple of decades – an apparent outbreak or epidemic – an 'emerging pathogen'. Many cases certainly remain unreported; in the last few years, the CDC has used various means to estimate true numbers, but some researchers believe these estimates are still much too low.
Public health concerns have become wide-spread
Proximal causation: The disease – the symptoms we experience under the name 'Lyme disease' – is induced by infection with a spirochaete bacterium (in the same group as the bacterium that causes syphilis). The proper name of the disease is borreliosis. But a 'disease' is just a collection of symptoms...
Recent genetic analyses show that the Ötzi the Iceman – a mummy preserved beneath a glacier in the European Alps for about 5300 years carried *Borrelia*. Further genetic analyses of *Borrelia* itself suggest that the species originated in Europe and is quite ancient. It is not, as had been supposed, a 'new' pathogen from North America (although it may have evolved greater virulence recently here).
Causality at one remove: The bacterium is vector-transmitted – it must be transferred between hosts via a bite by the deer tick *Ixodes scapularis*. Ticks must, in turn, acquire the bacterium from a previous host. Ticks hatch as larvae without infection; in order to pass to the next life-cycle stage – the nymph – larvae must successfully gorge on blood from a mammal or bird host. Ticks seeking a host (‘questing’) perch on grass, twigs or weeds and simply wait; when a suitable host brushes past, they quickly release and attach to the host. They can wait for months. Nymphs must have a blood meal to molt and become adults. Adult females must have a blood meal to reproduce. If the tick acquires *Borrelia* from its first or second host, it can transfer it to the next host.
The tick's life-cycle has four stages; egg, larva, nymph, and (reproductive) adult. The life-cycle is typically extended over two years. Ticks can pick up the bacterium in year one and infect a new host in second year.
White-footed mice or deer mice (genus *Peromyscus*) are the most common and ubiquitous mammal in eastern woodlands and forests. They are also the ‘competent reservoir’ of *Borrelia*, meaning that the bacterium can persist and thrive in the mouse population from which it can be transferred to other species. A large proportion of deer mice are infected with the bacterium, which doesn’t appear to cause disease symptoms in the mice, and it is readily transferred to ticks feeding on the mice. Deer mice cause Lyme disease… But what regulates the abundance of deer mice (and so the likelihood of a tick using a deer mouse as one of its first hosts)? What do deer mice eat?
“MNKA” = 'minimum number known alive' Read the graph caption and make sure you understand what it is showing.
A favored food for deer mice (and many other species), when available, is acorns. Acorns are highly nutritious and easily stored. However they are not produced in constant quantities. Typically, an oak tree will produce very large crops every few years and virtually none in the intervening years.

In a year like this, one acre of oak woodland can yield a quarter-ton or more of nuts and these acorns are a source of sustenance for nearly 100 different forms of wildlife. One researcher actually tracked 15,000 acorns produced by one oak tree, and his work showed the following results: 87 percent of the acorns were harvested by mammals, 6 percent by insect predators (such as birds), 10 percent were naturally defective, and less than 1 percent actually sprouted, half of which died while they were still seedlings.

Black bear, white-tailed deer, grey squirrels, wood ducks, and turkeys (221 large acorns were found in a single turkey crop) were among the animals most dependent upon acorns as a food source.

- Vermont Guardian, November 2005
Oak trees in a particular area tend to exhibit synchrony in their acorn production patterns. Years when most trees produce large crops of nuts are called “mast” years (the word is an old English term for ‘meaty’ fruits produced by trees).
And oaks of the same species in one region tend to be synchronized in their fruiting ‘pulses’. This is referred to as ‘mast fruiting’ (because farmers used to rely on such crops of tree nuts to feed livestock, and they called this food source ‘mast’). Many types of trees that produce large seeds or fruit mast. WHY DO THEY DO THIS?
The prevailing theory for the EVOLUTIONARY reason for mast fruiting is the ‘predator satiation’ hypothesis. Seed-eater populations are limited in the ‘sparse’ years to levels that can’t consume all of the available nuts in mast years; some nuts ‘escape’ predation to produce new trees. Thus, individual trees that mast, and individuals that respond to the same ‘cues’ for a mast crop as other trees in the area, are most likely to produce seeds that survive to make new trees (i.e., these traits will be selected for). This is the predator satiation hypothesis. Some evidence supports it (i.e., conforms with predictions that emerge from the hypothesis).
Adding oak mast dynamics to the picture may explain fluctuations in Lyme disease frequency from year to year. Is it appropriate to say that oaks cause Lyme disease?
Pigs eating acorns, being watched by stern dog and a ham actor. A tangential comment; a number of organisms may have evolved as specialists in exploiting resources that are extremely abundant when they occur, but that occur infrequently (‘pulsed resources’). Pigs may be one of these (check out Dan Janzen's *Why do bamboos wait so long to flower*). Certainly human pig-herders have long recognized and exploited the phenomenon of masting to fatten their hogs.
THESE PATTERNS have been used to suggest a HYPOTHESIS FOR WHY LYME DISEASE HAS BECOME SUCH A PROBLEM ONLY RECENTLY (or did we just not notice it before)? Consider what’s changed. For example, passenger pigeons were another species that evolved to exploit resources that are occasionally extremely abundant (in this case by being able to travel great distances in huge flocks to where a resource ‘pulse’ might be available at any given time). They are known to have eaten really vast quantities – millions of tons -- of mast crops. Maybe they consumed the acorns before the mice could get them – in which case extinction of pigeons → increasing mouse populations → greater prevalence of *Borrelia burgdorferi*? 
Let us now, kind reader, inspect their place of nightly rendezvous. One of these curious roosting-places, on the banks of the Green river in Kentucky, I repeatedly visited. … I rode through it upwards of forty miles, and, crossing it in different parts, found its average breadth to be rather more than three miles. … I arrived there nearly two hours before sunset. Few Pigeons were then to be seen, but a great number of persons, with horses and wagons, guns and ammunition, … Two farmers from the vicinity of Russelville, distant more than a hundred miles, had driven upwards of three hundred hogs to be fattened on the pigeons which were to be slaughtered. … The dung lay several inches deep, covering the whole extent of the roosting-place. Many trees two feet in diameter, I observed, were broken off at no great distance from the ground; and the branches of many of the largest and tallest had given way, as if the forest had been swept by a tornado ….. Suddenly there burst forth a general cry of "Here they come!" The noise which they made, though yet distant, reminded me of a hard gale at sea, passing through the rigging of a close-reeded vessel. As the birds arrived and passed over me, I felt a current of air that surprised me. Thousands were soon knocked down by the pole-men. The birds continued to pour in. The fires were lighted, and a magnificent, as well as wonderful and almost terrifying, sight presented itself. The Pigeons, arriving by thousands, alighted everywhere, one above another, until solid masses were formed on the branches all round. Here and there the perches gave way under the weight with a crash, and, falling to the ground, destroyed hundreds of the birds beneath, forcing down the dense groups with which every stick was loaded. It was a scene of uproar and confusion. I found it quite useless to speak, or even to shout to those persons who were nearest to me. Even the reports of the guns were seldom heard, and I was made aware of the firing only by seeing the shooters reloading.

No one dared venture within the line of devastation. … The Pigeons were constantly coming, and it was past midnight before I perceived a decrease in the number of those that arrived. The uproar continued the whole night; …. Towards the approach of day, the noise in some measure subsided: …, the Pigeons began to move off in a direction quite different from that in which they had arrived the evening before, and at sunrise all that were able to fly had disappeared. The howlings of the wolves now reached our ears, and the foxes, lynxes, cougars, bears, raccoons, opossums and pole-cats were seen sneaking off, whilst eagles and hawks of different species, accompanied by a crowd of vultures, came to supplant them, and enjoy their share of the spoil.

It was then that the authors of all this devastation began their entry amongst the dead, the dying, and the mangled. The Pigeons were picked up and piled in heaps, until each had as many as he could possibly dispose of, when the hogs were let loose to feed on the remainder.

-J. J. Audubon

John James Audubon’s comments on the extreme abundance of passenger pigeons
Let us take a column of one mile in breadth, which is far below the average size, and suppose it passing over us without interruption for three hours, at the rate mentioned above of one mile in the minute. This will give us a parallelogram of 180 miles by 1, covering 180 square miles. Allowing two pigeons to the square yard, we have one billion, one hundred and fifteen millions, one hundred and thirty-six thousand pigeons in one flock. As every pigeon daily consumes fully half a pint of food, the quantity necessary for supplying this vast multitude must be eight millions seven hundred and twelve thousand bushels per day.

- *J.J. Audubon* 1813
ADD DEER: Because the tick that is the vector for *Borellia* is called a ‘deer tick’, people tend to assume deer are the actual source of the disease. It’s a bad rap. Deer don’t carry the bacterium much (it doesn’t seem to thrive in their blood), BUT they often host many ticks of all ages, including gravid adult females. And deer can travel large distances carrying their ticks along for the ride. And they like acorns a lot. Because they are large and mobile, deer TRACK food pulses spatially. In mast years they travel to oak forests to feed on acorns, where the gravid female ticks they’re carrying can drop to the ground and lay eggs that will hatch the following spring. When they are likely to find one of the now-abundant deer mice as their larval host, and acquire the bacterium… Do DEER CAUSE LYME DISEASE?
The more nuts available, the less deer travel (this is a prediction of ‘optimal foraging theory’, a central ecological concept that emerges from game theory).
But small, local populations of things like rodents and song birds can't 'follow' the crop; instead their populations respond **NUMERICALLY**, increasing dramatically in response to mast years and crashing between.
Following mast years, deer mice produce larger litters of young more frequently. They breed through the winter, feeding on stored acorns, when normally they stop breeding due to scarcity of food by late winter and populations crash before spring. Following mast years, deer mouse populations continue to increase through the winter and so, in spring, when tick eggs hatch and questing larvae are numerous, they’re very likely to encounter a deer mouse – the *Borrelia* reservoir – and become an infected nymph that might bite you. OAKS CAUSE LYME DISEASE… (NOTE that if this chain of reasoning – hypothesis – is correct, it would predict that Lyme disease cases should be more frequent about a year after a mast crop of acorns…)
A great deal of work on this system and how it relates to Lyme disease has been done in Rick Ostfeld's lab at the Institute for Ecosystem Studies in Millbrook, NY (in Dutchess County – the epicenter of Lyme disease). Many of the results reviewed here are from the work of Ostfeld and collaborators.
None of this happens in isolation; Garrett Hardin’s ‘first law of ecology’ is ‘you can’t do just one thing’. Deer mice are also predators on the eggs and young of song-birds that nest on the ground or in low shrubs. Do high population of hungry mice (in years right after mast crops) have negative effects on song-bird populations? Sharp-shinned hawks eat song-birds. Does the effect propagate up the food chain?
Maybe; an experiment with artificial nests
But it's odd that songbird breeding success is ALSO low in years following very low rodent populations. Is there another layer of feedback?
Avian predators also eat songbirds AND mice; perhaps their populations build up following rodent population surges, then when rodent populations crash (a year after mast), hungry hawks focus on song-birds? (This propagation of effects up and down the food-chain is common. Ecologists talk about 'top-down' and 'bottom-up' control on ecological structures. If acorn abundance is what controls all these populations, that would be an example of 'bottom-up' control...) Such complex feed-backs make system behavior very hard to model!
SONGBIRD POPULATIONS IN FLUCTUATING ENVIRONMENTS: PREDATOR RESPONSES TO PULSED RESOURCES

KENNETH A. SCHMIDT AND RICHARD S. ÖSTFELD
Institute of Ecosystem Studies, Box 437, Millbrook, New York 12546 USA

Daily nest mortality rates on songbird nests as a function of the summer rodent density (number of animals/2.25 ha).

**Fig. 4.** Sharp-shinned and Cooper's Hawk abundance (unadjusted to parity here) from 37 Christman Bird Count regions surrounding Dutchess County (New York), as a function of (a) current or (b) red oak acorn abundance measured at the Institute of Ecosystem Studies. Hawk abundances are plotted against rodent densities (number of animals/2.25 ha) from the previous season or against acorn densities (acorns/3.7 ha) from two previous seasons.
Fig. 5. Schematic diagram of the connections between arks, mast-consumming rodents, songbirds (thrushes in particular), and hawks. The figure goes through a nesting cycle (left to right) from low to intermediate to high acorn production. Positive and negative effects highlighted in the study are designated by solid and dashed arrows, respectively. The notations beside the arrows designate the period over which abundances were examined: $A_t = Autumn$ of year $t$, $S_{t+1} = Summer$ year $t + 1$, $W_{t+1} = Winter$ year $t + 1$. Songbirds have two negative inputs: rodents, primarily via nest predation, and hawks, primarily via predation on fledglings, juveniles, and adults.
But there are other changes in the landscape. In the 19th century the northeast was essentially completely deforested and large mammal populations (including deer) almost eliminated. Since then, forests have recovered with agricultural abandonment. Oaks are often a prominent component of post-agricultural forests in southern new england and the lower Hudson valley – the areas where Lyme is most prominent. LYME DISEASE IS CAUSED BY HUMAN SETTLEMENT AND LAND-USE?? (These maps for north-central Mass. show forest cover in green for 1830 and 1985; most of the northeast would show a similar pattern.)
BUT WHY HAS LYME disease become so much more serious NOW? Perhaps it's because passenger pigeons are gone, so rodent populations get larger – but that should have happened a century ago... Another aspect of the modern landscape of these regions is that forests are often highly FRAGMENTED – broken up by patterns of human settlement (farms or suburban development depending on area). Additionally, residential patterns have changed; for esthetic reasons, people choose to live in dispersed developments interspersed with wooded areas.
Fragmentation has many effects on the ecological structure of forest communities. For example, as forest patch size decreases, diversity of mammal species – potential hosts for ticks – decreases. But deer mice don’t require large patches and are present everywhere; in the smallest patches, they’re about the only mammal around. So, in small patches, tick larvae are most likely to attach to a mouse and become infected nymphs that can give you Lyme disease; in larger patches, larvae are likely to encounter other hosts, none of which are as likely to infect them with *Borrelia.*
And large patches of forests are more likely to support predators that will eat deer mice, while they're among the first to go extinct when habitat area shrinks.
So researchers have predicted that exposure to infected nympha tick is more likely in landscapes dominated by small forest patches. There's some evidence to support this, as well. SO, it seems that the risk of human infection is particularly high where humans live close to small, fragmented, isolated patches of forest. SUBURBANIZATION CAUSES LYME DISEASE?
The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk

Kathleen LoGiudice**, Richard S. Ostfeld*, Kenneth A. Schmidt**, and Felicia Keesing**

Fig 1. Predicted NIP across a realistic range of mouse densities as host diversity is increased and host community composition is concomitantly changed. Host community consisting of only white-footed mice (gray diamonds) (A) white-footed mice, chipmunks, and white-tailed deer (dark blue squares) (B), all hosts in B plus raccoons, opossums, and skunks (pink triangles) (C), all hosts in C plus short-tailed shrews and four species of ground nesting birds (light blue circles) (D), all hosts in D plus three squirrels and Shenone shrews (red triangles) (E), and field data collected at our site over 7 years, showing the mouse density during the local peak in year 1 and NIP for host-seeking nymphs in year 1 + 3 (yellow circles) (F).

Fig 2. The ability of each species to reduce the effect of white-footed mice (the most competent reservoir) on NIP. Dilution potential is the difference in percentage points between the expected NIP in a two-host community consisting of mice plus the focal species and a community in which mice are the only possible host. Sq., squam; S.t.s., short-tailed shrews; S.s., Shenone shrews; O, opossums; C, chipmunk; D, deer; B, birds; R, raccoon; M, mouse.
So human risk of Lyme disease is a function of exposure to tick nymphs or adults that have acquired *Borrelia* from a previous host. Can we take this a step further and see if the risk of Lyme disease can be quantitatively modeled/predicted? What are the factors that might increase risk? Can these be incorporated in quantitative structures and computer models?
It gets even more complicated as complexity is added to the food web. It appears that MEDIUM-SIZED predators – like coyotes (whose abundance has increased dramatically in the northeast in recent years) – can lead to decreased abundance of SMALL predators (like foxes, either eating or just competing with them. Foxes are mouse specialists, so reducing fox numbers may actually FAVOR deer mouse populations... COYOTES CAUSE LYME DISEASE?
Lyme disease frequencies are better predicted by COYOTE and FOX abundance than by DEER abundance. STUDY THESE GRAPHS and think about what they mean…
BUT WHY has this system changed in recent decades? Why the increase in coyotes? One possibility is the elimination, by humans, of wolves. Wolves tended to exclude coyotes from forested habitats – partly by hunting and eating them (even though they’re close relatives and can interbreed). Wolves are specialists on large prey, like deer, but they don’t bother things as small as foxes. So, replacing wolves with coyotes may ‘shift the state’ of the whole food chain (what’s sometimes called a ‘tipping point’ phenomenon, or a system with ‘alternative stable states’). It can be either ‘wolf and fox eat a lot of deer and mice (and maybe squirrels and rabbits benefit), OR ‘coyotes eat a lot of medium-sized animals like foxes, squirrels, rabbits, and deer and mice benefit’.

COYOTES CAUSE LYME DISEASE?
There are yet other dynamics linked to these processes that remain to be fully understood. For example, Gypsy moths are a non-indigenous species, introduced originally as a potential source of silk.
After intentional introduction as silk producers, they escaped confinement and have become one of our most problematic forest pests.
Gypsy moths are an ‘outbreaking’ species. Populations can fluctuate between very low background levels and occasional massive outbreaks that can cause landscape-scale defoliation of trees and, sometimes, significant tree mortality (certainly stress for the defoliated trees). There are a number of species of insects that have similar population cycles; they are not all introduced.
The causes of gypsy moth outbreaks have been a long-time object of study; they’re still not well understood, but I won’t get into that here (it’s an area that would be of interest for those who are mathematically inclined – one of the first 'real-world' applications of complexity theory).
Gypsy moth egg cases and cocoons can be extremely abundant when there’s an outbreak; deer mice love to eat them. So gypsy moths decrease oak vigor by defoliating trees, thus decreasing likelihood of a mast crop – but they also support larger deer mouse populations. Gypsy moths both cause and prevent Lyme disease. This is an example of a system with FEEDBACK LOOPS – a ‘complex system’ – and the behavior of such systems is extremely difficult to predict. All ecological systems have such feedback loops. (Mice are also a likely factor in helping to regulate gypsy moth populations; when large deer mouse populations are getting hungry in a summer AFTER a mast crop, they may really hit gypsy moth populations hard.)
Chain Reactions Linking Acorns to Gypsy Moth Outbreaks and Lyme Disease Risk
Clive G. Jones, Richard S. Ostfeld, Michele P. Richard, Eric M. Schauber, Jerry O. Wolff

In eastern U.S. oak forests, defoliation by gypsy moths and the risk of Lyme disease are determined by interactions among acorns, white-footed mice, moths, deer, and ticks. Experimental removal of mice, which eat moth pupae, demonstrated that moth outbreaks are caused by reductions in mouse density that occur when there are no acorns. Experimental acorn addition increased mouse density. Acorn addition also increased densities of black-legged ticks, evidently by attracting deer, which are key tick hosts. Mice are primarily responsible for infecting ticks with the Lyme disease agent. The results have important implications for predicting and managing forest health and human health.
So, a SMALL PART of all of this can be shown in a cause-effect diagram. A sort of *causal model (or hypothesis) of the system*. Here, signs indicate positive or negative population influences; if the organism at the bottom of the arrow increases, it will have the indicated effect on population of the organism at the other end. The signs change depending on resource (acorn) supply. Imagine what other links might exist (or have changed), and think about how you'd assess their importance.
The Lyme disease story touches on many of the kinds of questions ecologists ask. It’s hard to simplify what ecology is too far, but it’s possible to put most of those questions in one of three or four big categories:

BIG QUESTION ONE: DIVERSITY. What regulates diversity? Why do some areas support more species than others? What factors favor high diversity (what allows species to coexist?) or constrain diversity (what prevents species from coexisting?)? Are there patterns? Explanations? Does diversity have practical consequences for human well-being?
BIG QUESTION TWO: ABUNDANCE and DISTRIBUTION. What factors determine abundances and distributions of particular species? Ranges of species? Are there patterns? Predictions?
(Different types of ecosystems or *ecological communities* are ‘assembled’ as a result of factors that regulate species distributions and abundances. We intuitively interpret these assemblages to tell us things about they area/habitat; we are all applied ecologists…"
BIG QUESTION THREE: **BIOLOGICAL PRODUCTIVITY.** What factors control the rate of overall ecosystem processes – particularly the rates at which new organic material (biomass) is produced and consumed? What do patterns in rates of ecosystem production suggest?
BIG QUESTION FOUR: EVOLUTIONARY EFFECTS. What are the linkages between ecological and evolutionary processes and patterns? How is the diversity of life derived over evolutionary time?