Hosts as ecological traps for the vector of Lyme disease

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Vectors of infectious diseases are generally thought to be regulated by abiotic conditions such as climate or the availability of specific hosts or habitats. In this study we tested whether blacklegged ticks, the vectors of Lyme disease, granulocytic anaplasmosis and babesiosis can be regulated by the species of vertebrate hosts on which they obligately feed. By subjecting field-caught hosts to parasitism by larval blacklegged ticks, we found that some host species (e.g. opossums, squirrels) that are abundantly parasitized in nature kill 83–96% of the ticks that attempt to attach and feed, while other species are more permissive of tick feeding. Given natural tick burdens we document on these hosts, we show that some hosts can kill thousands of ticks per hectare. These results indicate that the abundance of tick vectors can be regulated by the identity of the hosts upon which these vectors feed. By simulating the removal of hosts from intact communities using empirical models, we show that the loss of biodiversity may exacerbate disease risk by increasing both vector numbers and vector infection rates with a zoonotic pathogen.

Keywords: zoonotic disease; host; vector; diversity; Lyme disease; infectious disease

1. INTRODUCTION

Worldwide, more than 1.3 million people die each year of infectious diseases transmitted by a vector, such as a mosquito, sand fly or tick (World Health Organization 2004). Vector-borne diseases also inflict heavy tolls on crops, livestock and wildlife (Daszak *et al.* 2000; Anderson *et al.* 2004). As a consequence, understanding variation in exposure risk to vector-borne diseases, and managing environments to reduce this risk, are important goals.

Vector abundance is a key determinant of risk of exposure to the pathogens that vectors transmit (Ginsberg 1993; Antonovics *et al.* 1995; Mather *et al.* 1996). The abundance of vectors can be determined by climate-driven population performance (Fish 1993; Randolph 1993; Martens *et al.* 1995; Lindgren *et al.* 2000; Rogers & Randolph 2000; Yang *et al.* 2008). Climate can regulate the abundance of arthropod vectors directly, e.g. by desiccation, freezing or overheating, or indirectly, e.g. by altering vegetation type and structure. However, despite some clear cases in which climate regulates vector abundance (Alto & Juliano 2001; Afrane *et al.* 2005, 2006; Yang *et al.* 2008), in many other cases climate fails to explain vector abundance or disease incidence (Reiter 2001; Schulze & Jordan 2005; Ostfeld *et al.* 2006).

For example, long-term population dynamics of black-legged ticks (*Ixodes scapularis*) in New York, USA were not associated with temperature (growing degree-days) or precipitation parameters (Ostfeld *et al.* 2006). Alternatively, abundance of vectors that are host- or habitat-specialists can be regulated by the availability of specific hosts (e.g. fleas on prairie dogs; Gage & Kosoy 2005) or breeding sites (e.g. tree-hole mosquitoes; Juliano 2007). However, most vectors of zoonotic pathogens are host- and habitat-generalists, that is, they feed on a variety of host species and occupy different habitat types (Ostfeld & Keesing 2000; Molyneux 2003). For these species, vector survival and abundance might depend most strongly on the community of host species upon which they feed.

Host species can differ dramatically in their quality as a reservoir, that is, in their probability of infecting a feeding vector with a specific pathogen (Ostfeld & Keesing 2000 for review; Komar *et al.* 2002, 2003; LoGiudice *et al.* 2003). However, host species might also differ substantially in their quality as a host, here defined as the probability that a vector attempting a blood meal from that host successfully feeds and survives. Previous studies have documented that host quality does vary. For example, Ogden *et al.* (2004) found that adult female *I. scapularis* ticks that fed on raccoons had significantly shorter pre-oviposition periods than did ticks that fed on dogs. And Randolph (1979) showed that *Ixodes tranguliceps* ticks that fed on *Apodemus sylvaticus* were

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more likely to become engorged than were ticks that fed on laboratory mice when the hosts were repeatedly reinfested with ticks. Variation in host quality appears to be caused by differences in either host-immune response (Randolph 1979) or host grooming (Ostfeld & Lewis 1999; Shaw *et al.* 2003). If some host species that are abundantly parasitized in nature are of sufficiently low quality that they strongly reduce tick fitness compared with other hosts, then those poor quality hosts might act as ecological traps (Robertson & Hutto 2006).

Whenever host species differ strongly in host quality, the abundance of a generalist vector could be limited by the relative availabilities of the species comprising the host community—i.e. by the composition of the host community. Communities with a high proportion of poor-quality hosts would then be expected to produce smaller populations of vectors.

We investigated whether the identity of hosts determines survival of blacklegged ticks, which are vectors of Lyme disease (LD), granulocytic anaplasmosis and babesiosis, three widespread and emerging diseases in the US and Europe. LD, the most prevalent of the three and the best understood, is caused by a spirochete bacterium, *Borrelia burdorferi*, which is passed from one host to the other by the bite of an infected ixodid tick. In the northeastern and mid-western US and eastern Canada, the vector is the blacklegged tick, *I. scapularis*. Larval ticks feed on a wide variety of vertebrate hosts, including mammals, reptiles and birds (Keirans *et al.* 1996). Within LD endemic zones of the northeastern US, larval ticks commonly feed on at least 15 species of forest mammals and ground-dwelling birds (LoGiudice *et al.* 2003). Larvae that feed successfully molt into the nymphal stage, which overwinters before seeking a host the following late spring or early summer. The population density of nymphal ticks, and that of infected nymphal ticks, are key ecological risk factors in the LD epidemic (Lane *et al.* 1991; Barbour & Fish 1993; Ostfeld & Keesing 2000).

To determine if the composition of the host community could affect tick survival, we experimentally determined the proportion of ticks that fed successfully on each of six host species. Then we combined these results with data on tick burdens and reservoir competence of hosts to parameterize a model for how the loss of host species, alone or in combination, from ecological communities would affect the density of infected nymphal ticks (DIN).

2. MATERIAL AND METHODS

(a) *Capturing and holding hosts*

In August and early September 2008, during the peak of the questing period for larval ticks, we captured six commonly parasitized species of hosts at our forested field sites at the Cary Institute of Ecosystem Studies in Millbrook, New York. Hosts were white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), grey squirrels (*Sciurus carolinensis*), opossums (*Didelphis virginiana*), veeries (*Catharus fuscescens*) and catbirds (*Dumetella carolinensis*). Details of the trapping procedures are available as electronic supplementary material. After capture, animals were transported to the Rearing Facility at the Cary Institute of Ecosystem Studies. Animals were then placed in

appropriately sized cages (details in electronic supplementary material), and supplied with food and water ad libitum. All cages had floors of wire mesh or parallel wires. These cages were held over dishpans containing layers of moistened paper towels, with a border of petroleum jelly placed around the interior of the pan to prevent ticks from climbing out (Sonenshine 1993). Paper towels were examined exhaustively every 24 h to count all ticks that had dropped off the host. Hosts were kept under these conditions for 72 h, which was long enough for most larval ticks to feed to repletion. There were no differences among host species in the rates at which ticks fed (figure 1 in the electronic supplementary material).

(b) *Reinfesting hosts*

After the 72 h pre-test period, each host was inoculated with 100 larval ticks that had been either collected in the field or hatched from eggs in the laboratory. Larvae hatched from eggs in the laboratory were the offspring of locally collected adult ticks fed on rabbits. Mice and birds were restrained by hand during inoculation; all other hosts were restrained in nylon mesh-handling cones. Inoculations were conducted by placing the 100 ticks, which had been pre-counted and placed in plastic vials, on the host's neck and head with a number 00 paintbrush. Brushes were checked carefully to ensure that no ticks remained on the brush after inoculation. After inoculation, the host was placed in a motion-restricting chamber for 4 h to allow the larvae time to attach without being immediately groomed off. The chambers consisted of appropriately sized PVC pipe (3.2 cm diameter for mice, 5 cm diameter for chipmunks and veeries, 7.6 cm diameter for grey squirrels and grey catbirds, 10 cm diameter for small opossums, and 15.2 cm diameter for larger opossums) with holes drilled through for air circulation. Organdy fabric was used to cover the holes to prevent ticks from leaving the chamber, and the ends of each pipe were tightly capped. Food was placed in each chamber (apple slices for mice, chipmunks, squirrels and opossums; honeysuckle berries for birds) as a source of food and moisture during their restraint.

Hosts were then returned to their individual cages, which were suspended over pans of moist paper towels for collecting ticks. We did not attempt to control for prior exposure of hosts to feeding ticks, which potentially can affect subsequent tick feeding success (Levin & Fish 1998, but see Hazler & Ostfeld 1995), but because they were mature animals captured months after the beginning of the tick season at our sites, all hosts had prior experience with ticks. The number of larval ticks that fed from each individual host was determined by counting ticks that dropped into pans every 24 h for 96 h following inoculation. We held animals for 96 h post-inoculation because data from these host species indicated that few ticks remained on hosts after 4 days, and this value did not vary among species (figure 1 in the electronic supplementary material). Hosts were returned to their points of capture after tick collection was complete.

We categorized the original 100 ticks as replete; partially fed; chewed; and unfed (flat). Any ticks not accounted for directly were assumed to have been consumed or destroyed during grooming (Shaw *et al.* 2003). The number of larvae feeding to repletion (full or partial) was compared using a one-way analysis of variance (ANOVA) with host species as the treatment and individual hosts as replicates.

(c) *Building and parameterizing the model*

To quantify the impact on LD risk of host-specific vector survival rates, we adapted a previous model developed to quantify the impacts of host species on the proportion of infected nymphal ticks (Giardina *et al.* 2000; LoGiudice *et al.* 2003). Our model, which calculates the *density* of infected nymphal ticks, incorporates host-specific variation in observed tick burdens, tick survival rates, population density and reservoir competence. The DIN, which is the primary risk factor for LD is,

$$\mathrm{DIN} = \sum_{i=1}^{n} C_i B_i N_i,$$

where C_i is the proportion of larval ticks that get infected from successfully feeding on species i, B_i the average number of ticks that successfully feed on species i, N_i the density of host species i, and n the total number of species in the community. Data for C_i, the reservoir competencies, and B_i, the body burdens, of host species were determined from a combination of prior research by this group (LoGiudice *et al.* 2003), original data collected in summer 2008, and literature values (table 1). Values for N_i, the density of each host species, were obtained from a combination of our field studies and literature values (table 1).

(d) *Removing hosts*

We calculated DIN for a host community consisting of six species, and then removed each species individually to determine its specific impact on DIN. When a species was removed from our model, we calculated the number of larval ticks that that species would have 'trapped' as B_i/S_i, where S_i is the proportion of larval ticks that successfully feed on host i, as determined by our laboratory reinfestation experiment. The number trapped is the number of questing larval ticks that would be added to the system if host species i were removed; this number is the product of the proportion of ticks that feed successfully on each individual and the mean number of individuals of each species. To account for this increase in questing larval ticks, we then redistributed those larvae on the remaining host population in proportion to the percentage of the total tick population that each host, j, was already feeding:

$$\frac{B_j N_j}{\sum_{i=1}^{k} B_i N_i},$$

where k is the number of species remaining after host j is removed. Because little is known about the degree to which tick burdens on hosts vary as total host abundance varies, we allowed the percentage of ticks that were redistributed on the other hosts to vary from 0 to 100 per cent.

Because vertebrate host species do not appear to be lost from ecological communities at random, we also used our model to simulate the sequential loss of more than one species in an order determined by empirical observations of fragmented forest habitats (Ostfeld & LoGiudice 2003). The sequence of host removal was determined by a combination of observations from 40 forest fragments in the northeastern United States (LoGiudice *et al.* 2008) and observations of forest fragments in mid-western North America (Rosenblatt *et al.* 1999; Nupp & Swihart 2000; LoGiudice *et al.* 2003; Ostfeld & LoGiudice 2003). Veeries, which prefer forest interiors, were removed first, followed by opossums, which are medium-sized mammals that require

home ranges larger than many forest fragments, and then squirrels, chipmunks and catbirds. Mice were present in all runs of the model, reflecting results from forest fragments of the northeastern USA (LoGiudice *et al.* 2008).

3. RESULTS

(a) *Reinfestation experiment*

When hosts were experimentally inoculated with ticks in our experiment, most ticks stayed on the hosts to attempt to feed; fewer than 10 per cent dropped off in the apparatus. When ticks did drop off, however, there was no significant difference in the percentage that dropped off each host species (ANOVA on ranks, $p = 0.21$; figure 2 in the electronic supplementary material).

Species varied significantly in their quality as hosts for ticks ($p < 0.05$). Almost half of the larval ticks that were placed on white-footed mice fed to repletion, while only 3.5 per cent of ticks that fed on opossums did (figure 1). Eastern chipmunks, grey squirrels and the two species of birds—veeries and catbirds—were of intermediate quality. A small percentage of ticks were recovered unfed or partially engorged (table 1 in the electronic supplementary material). The remaining ticks were not recovered from their vertebrate hosts or from the apparatus that housed the hosts, indicating that they had been consumed during self-grooming.

These host-specific differences in feeding success became more pronounced when we took into account natural tick burdens. At our upstate New York sites, an average of 199 ± 90 (mean $\pm$ s.e.) replete larval ticks are collected from opossums caught in the wild during the larval activity peak (updated from LoGiudice *et al.* 2003 with data from the current study). But these larvae represent the 3.5 per cent that feed on opossums and survive—the vast majority (96.5%) of larval ticks that encounter an opossum and attempt to feed are apparently consumed. Working backwards, during any given week in the larval activity peak, each opossum must host more than 5500 larval ticks to produce 199 that successfully feed. By this logic, during the larval peak, each mouse encounters approximately 50 larval ticks per week, almost half of which feed to repletion and become nymphs. Thus, opossums in the host community serve as ecological traps for larval ticks, concentrating large numbers of larvae and then consuming them before they can feed and molt into nymphs (table 1).

(b) *Removing hosts*

The effect of removing individual host species was highly species-specific (figure 2). Removing mice, for example, always resulted in a substantial reduction in the density of infected nymphs, whereas the effect of removing squirrels could either modestly decrease or substantially increase DIN depending on the degree to which ticks were redistributed among the remaining hosts. If 33 per cent of ticks were redistributed, the loss of a single opossum (table 1) resulted in a 15 per cent increase in LD risk (figure 2). Greater rates of redistribution resulted in considerably higher DIN values.

When we removed more than one host species from the community, the DIN increased as more host species were removed. This result was obtained whenever more

Table 1. Parameter values, sample sizes and sources for feeding success, body burden of larval ticks, number of ticks trapped by each host (see main text), reservoir competence and density. (O, original data.)

| species	feeding success (S) mean (s.e.) (%)	n	body burden (B) mean (s.e.)	n	source	ticks trapped B/S	reservoir competence (C) mean (s.e.) (%)	n	source	density (n) number (ha^{-1})	source
mouse	49.3 (2.2)	20	24.6 (2.6)	43	O, LoGiudice et al. (2003)	50	92	15	O	40	O
squirrel	17.2 (4.6)	11	145.0 (73.2)	8	LoGiudice et al. (2003)	843	15	8	O	8.1	Williams (1936); Brown & Yeager (1945); Mosby (1969); Montgomery et al. (1975); Thompson (1978); Gurnell (1987); Merritt (1987)
chipmunk	24.3 (3.6)	17	22.2 (8.9)	37	O, LoGiudice et al. (2003)	91	55	20	O	20	O
veery	27.6 (3.1)	10	13.4 (4.3)	12	O	49	28	10	O	4.2	O
catbird	26.7 (4.5)	10	9.3 (2.0)	11	O	35	10	12	Ginsberg et al. (2005)	4.2	O
opossum	3.5 (1.5)	6	199.0 (90.2)	27	O, LoGiudice et al. (2003)	5686	3	18	O	1	Williams (1936); Lay (1942); Fitch & Sandidge (1953); Sanderson (1961); Holmes & Sanderson (1965); Merritt (1987); Whitaker & Hamilton (1998)
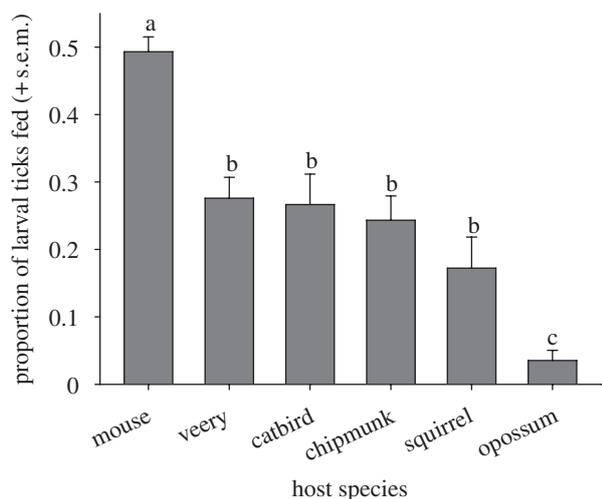
Figure 1. The proportion of larval ticks that fed successfully (+s.e.m.) on six species that are common hosts for larval blacklegged ticks (*Ixodes scapularis*) in upstate New York, USA. Hosts were captured in the field and held in the laboratory until ticks naturally feeding on them had fed to repletion and dropped off. Hosts were then reinfested with 100 larval ticks and monitored to determine the proportion of those ticks that fed successfully. Lowercase letters indicate results that were significantly different (one-way ANOVA; $p < 0.05$).

than 10 per cent of ticks that would have fed on missing hosts were redistributed on remaining hosts (figure 3).

4. DISCUSSION

The species identity of a host encountered by an unfed larval tick had a significant effect on the probability of tick survival. In our experiment, larval ticks that attempted to feed on white-footed mice were an order of magnitude more likely to survive than were ticks that attempted to feed on opossums. These results, combined with data on host abundance, natural tick burdens and reservoir competence, revealed that the effect of hosts on the DIN is highly species-specific. The removal of mice from a simulated community always reduced DIN while the removal of opossums increased DIN if the ticks that would have fed on the opossum were redistributed onto the remaining hosts. When species were removed sequentially in an order observed in field studies from the eastern United States, DIN increased as more species were lost from the community of hosts if the ticks that would have fed on the removed hosts were redistributed.

Our study design involved treating all hosts identically to minimize the potential for laboratory artefacts to produce interspecific differences. However, we were unable to control for all potential biases that could have affected results. For example, prior exposure to ticks can reduce tick feeding success (Randolph 1979). We did not directly account for species-specific differences in prior exposure, but all hosts in our experiment had been heavily infested with ticks prior to our experiments (table 1). Immune responses that directly kill ticks would have resulted in the recovery of differential numbers of unfed ticks in the apparatus, which did not occur (table 2 in the electronic supplementary material). However, the differences in
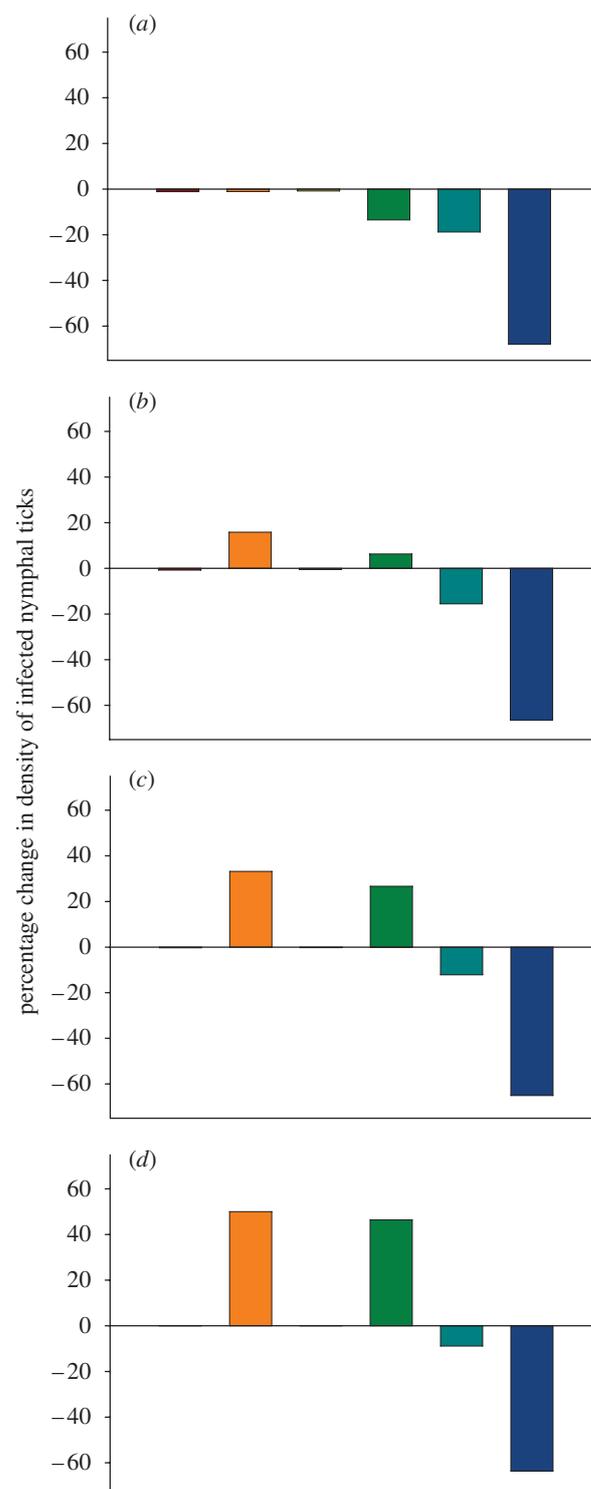

Figure 2. The percentage change in the density of infected nymphal ticks as host species (see legend) were removed individually from our model. Ticks that would have fed on the removed host species were redistributed on the remaining hosts: (*a*) 0 per cent; (*b*) 33 per cent; (*c*) 67 per cent; and (*d*) 100 per cent. Bars above zero indicate an increase in LD risk, while those below zero indicate a reduction in risk. Brown, no veeries; orange, no opossums; light green, no catbirds; dark green, no squirrels; aqua, no chipmunks; dark blue, no mice.

grooming efficacy that we observed might have been the result of species-specific differences in immune responses such as inflammation, which can stimulate or intensify grooming. Our initial restraint of the hosts in the
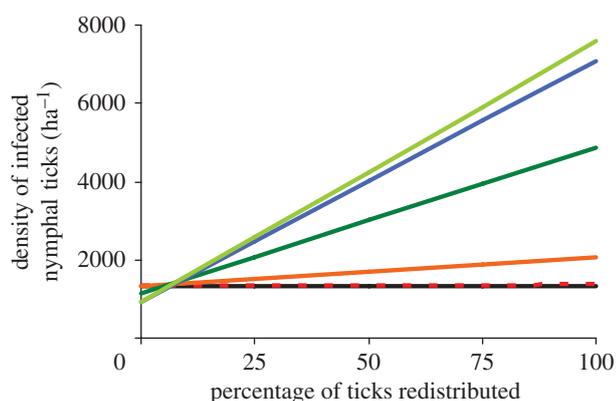
Figure 3. The density of infected nymphal ticks (DIN) per hectare as host species were removed sequentially from our model, when the ticks that would have fed on missing hosts were redistributed among remaining hosts from 0 to 100 per cent. Species were removed from the model in an order determined by empirical observations of the sequence of species loss in fragmented forest habitats. Veeries were removed first, followed by opossums, squirrels, chipmunks and then catbirds; white-footed mice were present in all communities (see main text). In habitats with two or more species lost, DIN was higher if ticks were redistributed on the remaining hosts, and greater rates of redistribution resulted in higher DIN values. Black line, intact; dotted orange lines, remove one species; continuous orange line, remove two species; dark green, remove three species; blue, remove four species; light green, remove five species.

laboratory might have biased our results if some host species are better able to groom off ticks upon encounter rather than later, after they attach. However, the reverse bias could have arisen if we had *not* restrained the hosts upon infestation.

Our model was parameterized almost entirely using data from our study site. As described in §2 and table 1, we used literature values to estimate the densities of opossums and grey squirrels. Density estimates for both of these species vary somewhat depending on location and methods, so we chose conservative estimates. For example, opossum densities in oak-hickory forest range from 0.9 to 2.5 per hectare; in this study and elsewhere (LoGiudice *et al.* 2003), we used 1 opossum ha^{-1} to parameterize the model. Our model results are insensitive to variation in host density within the range described in the literature (LoGiudice *et al.* 2003). Similarly, we used a sequence of species loss that combines data from our study sites with data from other published studies. This sequence should be considered provisional until better information on community disassembly rules becomes available (Ostfeld & LoGiudice 2003). However, data from 40 northeastern USA forest fragments confirm that white-footed mice are the only host species present at all sites (LoGiudice *et al.* 2008), from species-poor to species-rich. In such situations, the end result of species loss is that disease risk is highly elevated in habitats with the lowest host diversity.

The results of our model suggest that the loss of host species from an ecological community could increase LD risk if the ticks that would have fed on the lost species redistribute to the remaining hosts. Recent evidence demonstrates that decreases in the abundance of a specific host do cause substantial increases in the tick burdens on remaining hosts (Brunner & Ostfeld 2008), suggesting that redistribution in nature is substantial. Twelve years of data on six trapping grids in Dutchess County, NY, showed that as chipmunk density declined from 40 to 0, the number of ticks on mice increased by 15 larvae per mouse, an increase of approximately 50 per cent. Many important questions about redistribution remain to be resolved, including the degree to which redistribution of tick meals occurs across species and the key factors that cause temporal and spatial variation in redistribution.

In a recent synthesis, Robertson & Hutto (2006) define an 'ecological trap' as a habitat that an organism preferentially occupies and in which it has lower fitness than it would in an alternative available habitat. They define three criteria for identifying a trap. First, the organism must show a preference for that habitat. Second, fitness must vary among habitats. And third, the organism must have equal or lower fitness in the preferred habitat compared with alternative habitats. In our study, we determined conclusively that the survival of the ticks varies among host species, which can be considered habitats. We also showed that fitness is lower for ticks on opossums and squirrels than on alternative host species like mice. The question of preference is harder to characterize in this system. The mean number of successful tick meals on individual opossums (199) and squirrels (145) is five to eight times greater than the number on individual mice (25). Our calculations indicate that *attempted* meals on opossums exceeded those on mice by two orders of magnitude (table 1). These data suggest that ticks might prefer opossums and squirrels over mice, although true preferences are difficult to assess without controlled assessments of host choice. Opossums and squirrels seem to meet the criteria of ecological traps as described by Robertson & Hutto (2006).

Given the high mortality of ticks on opossums and squirrels, one might expect ticks to evolve the ability to detect and avoid feeding upon these hosts. In this case, inoculating these hosts with ticks might overestimate true mortality rates in nature. Two lines of evidence suggest that this is not the case. The first is the sheer number of larval ticks that feed to repletion on these hosts, as described above. The second is the number of ticks recovered from the apparatus used to inoculate the hosts with ticks. Ticks placed on hosts were not more likely to drop-off of opossums or squirrels than off of mice or any other species. Ticks might fail to drop-off low-quality hosts because they cannot detect host quality. Evidence indicates that larval ticks can discriminate only modestly among hosts (Shaw *et al.* 2003), though this issue has not been thoroughly investigated. Another possible explanation is that the daily mortality rate while larvae are questing for hosts is sufficiently high that attempting to feed on any host leads to a higher probability of survival than does waiting to encounter an optimal host. High seasonal attrition rates in densities of questing larvae suggest that field mortality may be high (Fish 1993; Ostfeld *et al.* 1996), supporting this hypothesis.

Opossums and squirrels played large roles in determining DIN in our model for several reasons. First, they trap large numbers of larval ticks, as our experiment revealed.

Both species are also relatively poor reservoirs for *B. burgdorferi*, with opossums and squirrels infecting, respectively, only 3 per cent and 15 per cent of ticks that feed successfully (table 1). Indeed, we found a significant positive correlation between the quality of our six species as hosts for vectors, measured as the proportion of larvae that successfully feed to repletion, and their competence as reservoirs, measured as the proportion of successfully feeding ticks that become infected with the pathogen ($R = 0.85$, $p = 0.03$). Further investigation will determine whether this relationship holds for other species in the LD system and whether a similar relationship occurs in other vector-borne disease systems.

One ecological feature that might make white-footed mice an optimal host for both vectors and pathogens is their ubiquity (Ostfeld & Keesing 2000). A recent study of 40 forest fragments in the northeastern US found that mice were the only vertebrate species occurring in all fragments (LoGiudice *et al.* 2008). The order in which species are lost is harder to predict (Ostfeld & LoGiudice 2003). Multiple lines of evidence suggest that larger mammals are among the first species to disappear as forest fragments become smaller and, consequently, as diversity declines (Rosenblatt *et al.* 1999; Ostfeld & LoGiudice 2003; LoGiudice *et al.* 2008). Consistent with these results, a previous study demonstrated a negative relationship between forest fragment size and several measures of LD risk (Allan *et al.* 2003). Presumably, the smallest fragments had a predominance of white-footed mice, which caused an increase in both tick infection prevalence and the density of infected ticks. But the study did not provide evidence for specific mechanisms. Our results suggest that smaller fragments may have lost species that regulate vector abundance, a mechanism that has been proposed (Keesing *et al.* 2006) but never demonstrated to reduce disease risk.

As species are lost from a community, the ticks that would have fed on them may (or may not) redistribute themselves on other hosts. Given that larval blacklegged ticks are extreme host-generalists (Keirans *et al.* 1996; LoGiudice *et al.* 2003), we expect such redistribution to accompany species losses. Our model incorporates this effect. It does not, however, incorporate changes in the abundance of the remaining host species, as might occur if a competitor or predator was removed. For example, the loss of chipmunks could result in increases in the abundance of mice, because mice and chipmunks are both small, granivorous rodents that compete for food resources. If the density of remaining hosts increases as diversity declines, increases in LD risk with species loss would be even greater than predicted by our model.

A number of studies have now shown that diversity reduces disease risk for both vector-borne and non-vector-borne diseases, including West Nile virus encephalitis (Ezenwa *et al.* 2006, 2007; Swaddle & Calos 2008; Allan *et al.* 2009), bartonellosis (Telfer *et al.* 2005), schistosomiasis (Johnson *et al.* 2009) and hantavirus pulmonary syndrome (Mills 2005; Suzán *et al.* 2009). But an understanding of the mechanisms behind this phenomenon has lagged behind and been controversial (Keesing *et al.* 2006; Begon 2008; Salkeld *et al.* 2008). This study demonstrates a specific mechanism—a reduction in vector abundance—by which diversity can reduce disease risk. Our results suggest that

maintenance of species that serve as ecological traps may be an important component of management efforts to mitigate vector-borne disease transmission.

REFERENCES

Afrane, Y. A., Lawson, B. W., Githeko, A. K. & Yan, G. 2005 Effects of microclimatic changes caused by land use and land cover on duration of gonotrophic cycles of *Anopheles gambiae* (Diptera: Culicidae) in Western Kenya highlands. *J. Med. Entomol.* **42**, 974–980. (doi:10.1603/0022-2585(2005)042[0974:EOMCCB]2.0.CO;2)

Afrane, Y. A., Zhou, G., Lawson, B. W., Githeko, A. K. & Yan, G. 2006 Effects of microclimatic changes caused by deforestation on the survivorship and reproductive fitness of *Anopheles gambiae* in Western Kenya highlands. *Am. J. Trop. Med. Hyg.* **74**, 772–778.

Allan, B. F., Keesing, F. & Ostfeld, R. S. 2003 The effect of habitat fragmentation on Lyme disease risk. *Conserv. Biol.* **17**, 267–272. (doi:10.1046/j.1523-1739.2003.01260.x)

Allan, B. F. *et al.* 2009 Ecological correlates of risk and incidence of West Nile virus in the United States. *Oecologia* **158**, 699–708. (doi:10.1007/s00442-008-1169-9)

Alto, B. & Juliano, S. A. 2001 Precipitation and temperature effects on populations of *Aedes albopictus* (Diptera: Culicidae): implications for range expansion. *J. Med. Entomol.* **38**, 646–656.

Anderson, P. K., Cunningham, A. A., Pater, N. G., Morales, F. J., Epstein, P. R. & Daszak, P. 2004 Emerging infectious diseases of plants: pathogen pollution, climate change and agrotechnology drivers. *Trends Ecol. Evol.* **19**, 535–544. (doi:10.1016/j.tree.2004.07.021)

Antonovics, J., Iwasa, Y. & Hassell, M. 1995 A generalized model of parasitoid, venereal, and vector-based transmission processes. *Am. Nat.* **145**, 661–675. (doi:10.1086/285761)

Barbour, A. G. & Fish, D. 1993 The biological and social phenomenon of Lyme disease. *Science* **260**, 1610–1615. (doi:10.1126/science.8503006)

Begon, M. 2008 Effects of host diversity on disease dynamics. In *Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems* (eds R. S. Ostfeld, F. Keesing & V. T. Eviner), pp. 12–29. Princeton, NJ: Princeton University Press.

Brown, L. G. & Yeager, L. E. 1945 Fox squirrels and gray squirrels in Illinois. *Il. Nat. Hist. Surv. Bull.* **23**, 449–536.

Brunner, J. & Ostfeld, R. S. 2008 Multiple causes of variable tick burdens on small-mammal hosts. *Ecology* **89**, 2259–2272. (doi:10.1890/07-0665.1)

Daszak, P., Cunningham, A. A. & Hyatt, A. D. 2000 Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* **287**, 443–449. (doi:10.1126/science.287.5452.443)

Ezenwa, V. O., Godsey, M. S., King, R. J. & Guptill, S. C. 2006 Avian diversity and West Nile virus: testing associations between biodiversity and infectious disease risk.

Proc. R. Soc. B **273**, 109–117. (doi:10.1098/rspb.2005.3284)

Ezenwa, V. O., Milheim, L. E., Coffey, M. F., Godsey, M. S., King, R. J. & Guptill, S. C. 2007 Land cover variation and West Nile virus prevalence: patterns, processes, and implications for disease control. *Vector-Borne Zoonot.* **7**, 173–180. (doi:10.1089/vbz.2006.0584)

Fish, D. 1993 Population ecology of *Ixodes damini*. In *Ecology and environmental management of Lyme disease* (ed. H. Ginsberg), pp. 25–42. New Brunswick, NJ: Rutgers University Press.

Fitch, H. S. & Sandidge, L. L. 1953 Ecology of the opossum on a natural area in northeastern Kansas. *Univ. Kansas Publ. Mus. Nat. Hist.* **7**, 305–338.

Gage, K. L. & Kosoy, M. Y. 2005 Natural history of plague: perspectives from more than a century of research. *Annu. Rev. Entomol.* **50**, 505–528. (doi:10.1146/annurev.ento.50.071803.130337)

Giardina, A. R., Schmidt, K. A., Schauber, E. M. & Ostfeld, R. S. 2000 Modeling the role of songbirds and rodents in the ecology of Lyme disease. *Can. J. Zool.* **78**, 2184–2197. (doi:10.1139/cjz-78-12-2184)

Ginsberg, H. S. 1993 *Ecology and environmental management of Lyme disease*. Piscataway, NJ: Rutgers University Press.

Ginsberg, H. S., Balmforth, M. G., Zhioua, E., Mitra, S. & Buckley, F. G. 2005 Reservoir competence of native North American birds for the Lyme disease spirochete, *Borrelia burgdorferi*. *J. Med. Entomol.* **42**, 445–449. (doi:10.1603/0022-2585(2005)042[0445:RCONNA]2.0.CO;2)

Gurnell, J. 1987 *The natural history of squirrels*. New York, NY: Facts on File Publications.

Hazler, K. & Ostfeld, R. S. 1995 Larval density and feeding success of *Ixodes scapularis* on two species of *Peromyscus*. *J. Parasitol.* **81**, 870–875. (doi:10.2307/3284032)

Holmes, A. C. V. & Sanderson, G. C. 1965 Populations and movements of opossums in East-central Illinois. *J. Wildl. Manage.* **29**, 287–295. (doi:10.2307/3798433)

Johnson, P. T. J., Lund, P. J., Hartson, R. B. & Yoshino, T. P. 2009 Community diversity reduces *Schistosoma mansoni* transmission, host pathology, and human infection risk. *Proc. R. Soc. B* **276**, 1657–1663. (doi:10.1098/rspb.2008.1718)

Juliano, S. A. 2007 Population dynamics. In *Biorational control of mosquitoes*. Supplement to the Journal of the Mosquito Control Association Bulletin No. 7, vol. 23 (ed. T. G. Floore), pp. 265–275. American Mosquito Control Association.

Keesing, F., Holt, R. D. & Ostfeld, R. S. 2006 Effects of species diversity on disease risk. *Ecol. Lett.* **9**, 485–498. (doi:10.1111/j.1461-0248.2006.00885.x)

Keirans, J. E., Hutcheson, H. J., Durden, L. A. & Klompen, J. S. H. 1996 *Ixodes scapularis* (Acari: Ixodidae): redescription of all active stages, distribution, hosts, geographical variation, and medical and veterinary importance. *J. Med. Entomol.* **33**, 297–318.

Komar, N., Panella, N. A., Langevin, S. A., Brault, A. C., Amador, M., Edwards, E. & Owens, J. 2002 Avian hosts for West Nile virus in St. Tammany Parrish, Louisiana. *Am. J. Trop. Med. Hyg.* **73**, 1031–1037.

Komar, N., Langevin, S., Hinten, S., Nemeth, N., Edwards, E., Hettler, D., Davis, B., Bowen, R. & Bunning, M. 2003 Experimental infection of north American birds with the New York 1999 strain of West Nile virus. *Emerg. Infect. Dis.* **9**, 311–322.

Lane, R. S., Piesman, J. & Burgdorfer, W. 1991 Lyme borreliosis: relation of its causative agent to its vectors and hosts in North America and Europe. *Annu. Rev. Entomol.* **36**, 587–609. (doi:10.1146/annurev.en.36.010191.003103)

Lay, D. W. 1942 Ecology of the opossum in eastern Texas. *J. Mammal.* **23**, 147–159. (doi:10.2307/1375067)

Levin, M. L. & Fish, D. 1998 Density-dependent factors regulating feeding success of *Ixodes scapularis* larvae (Acari: Ixodidae). *J. Parasitol.* **84**, 36–43. (doi:10.2307/3284526)

Lindgren, E., Talleklint, L. & Polfeldt, T. 2000 Impact of climatic change on the northern latitude limit and population density of the disease-transmitting European tick *Ixodes ricinus*. *Environ. Health Perspect.* **108**, 119–123. (doi:10.2307/3454509)

LoGiudice, K., Ostfeld, R. S., Schmidt, K. A. & Keesing, F. 2003 The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proc. Natl Acad. Sci. USA* **100**, 567–571. (doi:10.1073/pnas.0233733100)

LoGiudice, K., Duerr, S., Newhouse, M., Schmidt, K. A., Killilea, M. & Ostfeld, R. S. 2008 Impact of community composition on Lyme disease risk. *Ecology* **89**, 2841–2849. (doi:10.1890/07-1047.1)

Martens, W. J. M., Niessen, L. W., Rotmans, J., Jetten, T. H. & McMichael, A. J. 1995 Potential impact of global climate-change on malaria risk. *Environ. Health Perspect.* **103**, 458–464. (doi:10.2307/3432584)

Mather, T. N., Nicholson, M. C., Donnelly, E. F. & Matyas, B. T. 1996 Entomologic index for human risk of Lyme disease. *Am. J. Epidemiol.* **144**, 1066–1069.

Merritt, J. F. 1987 *Guide to the mammals of Pennsylvania*. Pittsburgh, PA: University of Pittsburgh Press.

Mills, J. N. 2005 Regulation of rodent-borne viruses in the natural host: implications for human disease. *Arch. Virol.* **19**, 45–57.

Montgomery, S. D., Whelan, J. B. & Mosby, J. S. 1975 Bioenergetics of a woodlot gray squirrel population. *J. Wildl. Manage.* **39**, 709–717. (doi:10.2307/3800232)

Molyneux, D. H. 2003 Common themes in changing vector-borne disease scenarios. *Trans. R. Soc. Trop. Med. Hyg.* **97**, 129–132. (doi:10.1016/S0035-9203(03)90097-6)

Mosby, J. S. 1969 The influence of hunting on the population dynamics of a woodlot grey squirrel population. *J. Wildl. Manage.* **33**, 59–73. (http://dx.doi.org/10.2307/3799650)

Nupp, T. E. & Swihart, R. K. 2000 Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *J. Mammal.* **81**, 512–526. (doi:10.1644/1545-1542(2000)081[0512:LLCOSM]2.0.CO;2)

Ogden, N. H., Lindsay, L. R., Beauchamp, G., Charron, D., Maarouf, A., O'Callaghan, C. J., Waltner-Toews, D. & Barker, I. K. 2004 Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (Acari: Ixodidae) in the laboratory and field. *J. Med. Entomol.* **41**, 622–633.

Ostfeld, R. S. & Keesing, F. 2000 The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Can. J. Zool.* **78**, 2061–2078. (doi:10.1139/cjz-78-12-2061)

Ostfeld, R. S. & Lewis, D. N. 1999 Experimental studies of interactions between wild turkeys and blacklegged ticks. *J. Vector Ecol.* **24**, 182–186.

Ostfeld, R. S. & LoGiudice, K. 2003 Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* **84**, 1421–1427. (doi:10.1890/02-3125)

Ostfeld, R. S., Hazler, K. & Cepeda, O. 1996 Temporal and spatial dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a rural landscape. *J. Med. Entomol.* **33**, 90–95.

Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J. & Keesing, F. 2006 Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biol.* **4**, e145. (doi:10.1371/journal.pbio.0040145)

Randolph, S. E. 1979 Population regulation in ticks: the role of acquired resistance in natural and unnatural hosts. *Parasitology* **79**, 141–156. (doi:10.1017/S0031182000052033)

Randolph, S. E. 1993 Climate, satellite imagery and the seasonal abundance of the tick *Rhipicephalus appendiculatus* in southern Africa: a new perspective. *Med. Vet. Entomol.* 7, 243–258. (doi:10.1111/j.1365-2915.1993.tb00684.x)

Reiter, P. 2001 Climate change and mosquito-borne disease. *Environ. Health Perspect.* 109, 141–161. (doi:10.2307/3434853)

Robertson, B. A. & Hutto, R. L. 2006 A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87, 1075–1085. (http://dx.doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2)

Rogers, D. J. & Randolph, S. E. 2000 The global spread of malaria in a future, warmer world. *Science* 289, 1763–1766.

Rosenblatt, D. L., Heske, E. J., Nelson, S. L., Barber, D. M., Miller, M. A. & MacAllister, B. 1999 Forest fragments in east-central Illinois: islands or habitat patches for mammals? *Am. Mid. Nat.* 141, 115–123. (http://dx.doi.org/10.1674/0003-0031(1999)141[0115:FFIECI]2.0.CO;2)

Salkeld, D. J., Leonhard, S., Girard, Y. A., Hahn, N., Mun, J., Padgett, K. A. & Lane, R. S. 2008 Identifying the reservoir hosts of the Lyme disease spirochete *Borrelia burgdorferi* in California: the role of the Western Gray Squirrel (*Sciurus griseus*). *Am. J. Trop. Med. Hyg.* 79, 535–540.

Sanderson, G. C. 1961 Estimating opossum populations by marking young. *J. Wildl. Manage.* 25, 20–27. (doi.org/10.2307/3796986)

Schulze, T. L. & Jordan, R. A. 2005 Influence of meso- and microscale habitat structure on focal distribution of sympatric *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *J. Med. Entomol.* 42, 285–294. (doi:10.1603/0022-2585(2005)042[0285:IOMAMH]2.0.CO;2)

Shaw, M. T., Keesing, F., McGrail, R. & Ostfeld, R. S. 2003 Factors influencing the distribution of larval black-legged ticks on rodent hosts. *Am. J. Trop. Med. Hyg.* 68, 447–452.

Sonenshine, D. E. 1993 *The biology of ticks*, vol. 2. New York, NY: Oxford University Press.

Suzán, G. *et al.* 2009 Experimental evidence for reduced mammalian diversity causing increased hantavirus prevalence. *PLoS One* 4, e5461.

Swaddle, J. P. & Calos, S. E. 2008 Increased avian diversity is associated with lower incidence of human West Nile infection: observation of the dilution effect. *PLoS One* 3, e2488. (doi:10.1371/journal.pone.0002488)

Telfer, S., Bown, K. J., Sekules, R., Begon, M., Hayden, T. & Birtles, R. 2005 Disruption of a host–parasite system following the introduction of an exotic host species. *Parasitology* 130, 661–668. (doi:10.1017/S0031182005007250)

Thompson, D. C. 1978 The social system of the grey squirrel. *Behaviour* 64, 305–328. (doi:10.1163/156853978X00080)

Williams, A. B. 1936 The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6, 318–418. (doi:10.2307/1943219)

Whitaker, J. O. & Hamilton, W. J. 1998 *Mammals of the Eastern United States*. Ithaca, NY: Cornell University Press.

World Health Organization. 2004 The world health report: a changing history. Geneva, Switzerland: World Health Organization.

Yang, G.-J., Brook, B. W., Whelan, P. I., Cleland, S. & Bradshaw, C. J. A. 2008 Endogenous and exogenous factors controlling temporal abundance patterns of tropical mosquitoes. *Ecol. Appl.* 18, 2028–2040. (doi:10.1890/07-1209.1)

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