

Food Webs and Disease: Is Pathogen Diversity Limited by Vector Diversity?

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Abstract: Classical predator–prey and host–parasite systems have been extensively studied in a food web context. Less attention has been paid to communities that include pathogens and their vectors. We present a coarse-grained, pan-African analysis of the relationships between the abiotic environment (location, precipitation, temperature), the species richness and community composition of ixodid ticks, and the species richness and community composition of pathogens that ticks transmit to humans. We found strong correlations between the abiotic environment and tick species richness, and a weak but significant correlation between the abiotic environment and pathogen species richness. A substantial amount of variation in community composition of parasites and pathogens was not explained by the variables that we considered. A structural equation model that compensated for the indirect effects of climate on the pathogen community via tick community composition suggested that while the environment strongly regulates tick community composition and tick community composition strongly regulates pathogen community composition, abiotic influences on pathogen species richness and community composition are weak. Our results support the view that changes in the broader environment will influence tick-borne pathogens primarily via the influence of the environment on ticks. The interactions that regulate host–vector–pathogen dynamics are of particular relevance in understanding the relationships between environmental change and health concerns, such as the impact of climate change on the occurrence of vector-borne diseases.

Key words: Ixodidae, tick, pathogen, parasite, food web, biodiversity

INTRODUCTION

The study of trophic interactions has been an important source of insights in ecology. In recent years, trophic studies have moved beyond documenting patterns and towards understanding dynamic interactions and emergent effects (for instance, intraguild predation and top-down

regulation; Sih et al., 1998; Sukhdeo and Hernandez, 2005), as well as their consequences for such ecosystem functions as nutrient cycling (Naeem, 2002). During this period, there have been a number of revisions of accepted ideas about food web dynamics, including challenges to the classical assumption of rigidly separated trophic levels and an increasing recognition of the importance of indirect interactions between predators (e.g., Polis and Holt, 1992; Sih et al., 1998). However, while studies of predator–prey interactions and host–pathogen interactions have made

considerable progress in the last two decades, the field of pathogen community ecology is still in its infancy. In particular, there have been relatively few detailed case studies of vector–pathogen systems at the community level, and so the degree to which both classical and recent theories of food web dynamics are applicable to these systems has been uncertain (Dobson and Hudson, 1986; Marcogliese and Cone, 1997; Poulin, 1999). This is particularly true for dynamics that occur over broad spatial scales and longer time periods.

In this article, we draw together two unusually extensive data sets, one for the occurrences of pathogens and infectious diseases and the other for African ticks. The question of what determines pathogen community structure is of central importance for pathogen community ecology (Naeem, 2002) and, by extension, for the development of a more robust understanding of the consequences of environmental change for human wellbeing. We use the data to examine the broad-scale interactions between climatic conditions, the species richness and community composition of tick species, and the species richness and community composition of vector-borne pathogens in continental Africa.

Our central hypothesis in undertaking this study was that vector–pathogen communities should show nesting because organisms are most directly influenced by their immediate environment. In the case of ticks, many of which spend over 90% of their time off-host (Needham and Teal, 1991), the immediate environment is the abiotic environment; in the case of tick-borne pathogens, the immediate environment consists of ticks and their hosts. Consequently, we expected that the environment should influence ticks more strongly than it influences pathogens, while ticks should influence pathogens more strongly than does the environment. In addition, we reasoned that since many tick-borne pathogens are considered to be largely vector-specific (or are at least restricted to a small number of tick species; Wilson et al., 1990; Walker et al., 2000), the community composition and species richness of ticks should limit and, to some extent, determine the community composition of pathogens.

If our assumptions about mechanisms are correct, then the diversity of species in different trophic levels should be interdependent, not by multiple pathways but by direct up and down one-way links. We tested these predictions and found support for the idea that the vector–pathogen interaction in this instance is the dominant determinant of pathogen community composition, although abiotic context still appears to be important. Our results have some

interesting implications for food web theory, the control of vector-borne pathogens, and our understanding of the impacts of environmental change on emerging diseases.

METHODS

We obtained data on the occurrence of tick species, tick-borne parasitic diseases of humans, and a range of abiotic variables for each of 48 countries in continental Africa. The data used in the analysis are available on request from the authors.

Abiotic Data

The abiotic data were extracted in a GIS from a political map of Africa and estimates of temperature and rainfall from the year 1990. The original temperature and rainfall data were obtained from the Hadley Climate Center, via the global land cover model IMAGE (IMAGE-Team, 2001). The data were originally at a resolution of 0.5×0.5 degrees (approximately 50×50 km²). Values for all cells for which the center fell within the borders of a given country were averaged to produce a mean and a variance by country. The resulting data set included the following 55 abiotic variables: country area in km² (1 variable), mean and variance in X coordinate (2 variables), mean and variance in Y coordinate (2 variables), mean and variance of monthly precipitation (24 variables, two for each month), mean and variance of monthly temperature (24 variables as before), annual mean precipitation (1 variable), and annual mean temperature (1 variable).

The variables included in the analysis are those that we considered most appropriate for testing our central hypothesis. Guernier et al. (2004) have argued that climatic conditions, and more specifically rainfall range, have an important influence on pathogens. Cumming (1999, 2002) concluded that tick distributions at broad scales are primarily determined by climate. Previous work, however, has not established whether the observed relationship between pathogens and climate is a direct (i.e., climate-driven) or an indirect (i.e., vector-driven) effect. We included mean annual values because these provide some additional information that is not immediately represented in monthly data and may be of relevance to organisms, particularly those that (like many ticks) may live for several years. Country size is included as a rough correlate of sampling effort and to take into account the influence of the species-area relationship; and the X and Y coordinates (northing

and easting, in decimal degrees) provide some measure of the geographic location of countries relative to one another, allowing such possibilities as similarity in community composition due primarily to spatial autocorrelation to be considered. As might be expected, most of the abiotic data are highly correlated with one another, and so were analyzed using data reduction techniques (Principal Components Analysis [PCA] or Bray-Curtis ordination) that extract orthogonal variables from the larger matrix.

Tick Data

Tick data were assembled for the continent of Africa from a published data set that is fully described elsewhere (Cumming, 1998, 1999, 2000a, 2000b, 2002). The data consist of around 35,000 collection records assembled from a diverse array of published sources and museum collections. They span the African continent, although collection records in some countries are considerably more comprehensive than those in others. Tick occurrence data were extracted for 73 tick species in each of 48 countries. We used binary data for most of our analyses because spatially explicit occurrence data for the occurrence of pathogens were not available at the same grain. The binary data also have the advantage of being less influenced by collection effort and country size (note that the size of the country in square kilometers was included in the analysis as a potential explanatory variable).

The inclusion of 73 tick species in this analysis is somewhat arbitrary. It reflects the number of species (from a total African fauna of around 240 species) that have been sufficiently widely collected for us to be able to generalize in some way about their distributions. Our focus on more widely collected species means that statistical corrections for rare species are unnecessary for these data. Among the 73 tick species represented in this study are all of the major known vector species of tick-borne pathogens in Africa. We made no effort to exclude species that are not known to be vectors of pathogens, since the central issue of interest to us is the overall composition of the respective parasite and pathogen communities. The relationships between pathogens and ticks that are presented in this article would probably be stronger if only vector species were considered.

Data for Pathogens

Presence-absence data for 10 tick-borne pathogens from 48 continental African nations (i.e., excluding island nations) were compiled from the Global Infectious Disease and Epidemiology Network (GIDEON) Database (online at

<http://www.cyinfo.com>). Diseases not occurring on the African continent were excluded from the analysis. The list of tick-borne diseases includes the following: (1) Angiomatosis, due to bacterial *Bartonella* infections; (2) Tularemia, also called rabbit fever, which is a bacterial disease caused by the gram-negative pleomorphic bacterium *Francisella tularensis*; (3) Thogoto disease, which is caused by a virus belonging to the genus *Thogotovirus*; (4) African tick bite fever, a rickettsiosis caused by *Rickettsia africae*; (5) Relapsing fever, caused by a group of different *Borrelia* species; (6) Mediterranean spotted fever, also known as boutonneuse fever, for which the etiologic agent is *Rickettsia conorii*; (7) Crimean-Congo hemorrhagic fever (CCHF), a viral hemorrhagic fever of the *Nairovirus* group; (8) Babesiosis, also called piroplasmiasis, which is due to protozoan parasites of the genus *Babesia*; (9) Lyme disease, which is caused by *Borrelia burgdorferi* infection; and (10) Ehrlichiosis (human monocytic), a disease caused by *Anaplasma* organisms.

Each of these infectious organisms is generally transmitted to humans through the bite of a tick. *Amblyomma*, *Hyalomma*, *Rhipicephalus*, *Dermacentor*, *Ornithodoros*, and *Ixodes* are the tick genera that are primarily responsible for transmitting diseases to humans in Africa. The sheep tick *Ixodes ricinus* has been established as the primary vector of angiomatosis (Sanogo et al., 2003), whereas tularemia is transmitted to humans by *Dermacentor* species. *R. sanguineus*, *R. appendiculatus*, and *R. evertsi* (probably together with many other brown ticks) are vectors for thogotoviruses. Only ticks of the genus *Ornithodoros* transmit relapsing fever. Mediterranean spotted fever is transmitted by the dog tick *Rhipicephalus sanguineus*. Several tick species may transmit viruses causing Crimean-Congo Hemorrhagic Fever, but the most common vectors are *Hyalomma* and *Rhipicephalus* species. Babesiosis is transmitted by *Ixodes*, *Boophilus*, and *Rhipicephalus* species, and ehrlichiosis by *Amblyomma* and *Rhipicephalus* species, although other ixodid ticks may also be occasionally implicated in its transmission. In many cases, the detailed immune responses of different vectors and hosts to particular pathogens are still being worked out (Willadsen and Jongejan, 1999). The problem is complicated by the possibility that the transmission of human disease by tick species may be regulated as much by the habitat and host preferences of the tick as by its ability to transmit pathogens. For example, *R. appendiculatus* is frequently encountered on grass stems near to paths and attaches readily to humans, whereas many of the African *Argas*

species feed more frequently on birds (Cumming, 1998), and so are at their highest densities in bird nests and roosting sites where humans are much less likely to encounter them. In the absence of either controlled experiments or spatially explicit studies of the occurrence of African ticks and the pathogens that they carry, it is difficult to generalize about specialist versus generalist tendencies (Klompen et al., 1996, Cumming, 2004).

Risk factors for tick-borne diseases include living in an area with a lot of ticks, activities in suitable vegetation (such as high grasses), and frequent contact with animals. Tick-borne diseases are among the major factors that impede the development of rural economies in many African countries, through their impacts on livestock productivity and human health. Climatic conditions across the continent vary from tropical to temperate. While humidity and temperature determine the survival and activity of tick instars, temperature affects the rate of development and survival of both ticks and their parasites and carries important implications for the epidemiology of disease (e.g., Londt and Whitehead, 1972; Randolph and Rogers, 2000a).

General Treatment

Each data set was summarized to by-country format for the 48 countries that were initially considered. Western Sahara and Equatorial Guinea were removed from the analysis due to the paucity of available data, reducing the sample size to 46 countries. We treated each country as a separate and independent sampling location. We also assumed that the broad-scale nature of the analysis, the size of the data sets, the binary nature of the pathogen and tick data (presence–absence rather than abundance) and the fact that each data set was assembled in an internally consistent manner would compensate for differences in sampling effort between locations. Although both tick and pathogen data are likely to be biased by the quality of medical and veterinary research within a given country, the medical (human pathogen) and veterinary (tick and livestock pathogen) communities have largely done field sampling independently of one another in Africa; and the abiotic data are free of any sampling bias. Consequently, there is little scope for systematic bias in the analysis. This assumption is supported by previous analyses of tick–climate relationships (Cumming, 2000a, 2002), in which it was found that although tick-sampling effort differed significantly between countries, compensating for collecting effort did not

remove the significant relationship between tick occurrences and climate. Although no specific estimate of the impact of sampling effort on our results was undertaken in this article, we did include the area of each country and the mean and variance of the X and Y coordinates of all 50×50 cells falling within each country, so that country size and location would be taken into account in the analysis.

We first tested for correlations between pathogen species richness, tick species richness, and abiotic variation, using Spearman's rank correlation coefficient (Siegel and Castellan, 1988). Species richness was summarized for each of the 46 countries in the analysis for both pathogens and ticks. The bivariate correlations were undertaken in SPSS (SPSS, 1999). We then developed Structural Equation Models (SEM; see Shipley, 2002 for a thorough introduction) in the software package AMOS (Arbuckle, 2003). The SEM analysis used the two major components obtained from each data set by a Bray-Curtis ordination. Based on our hypothesis of nested dependence between diseases and their vectors, our expectation from this analysis was that we should see significant interactions between abiotic parameters and ticks, and between ticks and pathogens, but not necessarily between climate and pathogens.

RESULTS

A PCA ordination of the abiotic data matrix yielded five orthogonal variables that together explained 87% of the variance in the abiotic data. There were significant correlations between abiotic component 1 and pathogen species richness ($r_s = -0.375$, $P < 0.01$, $n = 46$) and between tick species richness and abiotic components 2, 3, and 5 ($r_s = 0.648$; $P < 0.000$, $r_s = 0.303$, $P < 0.041$; and $r_s = 0.416$; $P < 0.004$, respectively; $n = 46$ in all cases). All other correlations, including that between tick species richness and pathogen species richness, were insignificant at the $P = 0.05$ level. Applying a Bonferroni correction to these results does not affect their significance, with the one exception that the correlation between tick species richness and abiotic component 3 falls away.

We next considered the multivariate relationships between pathogens, ticks, and the environment using Structural Equation Modeling (SEM). The central hypothesis that we tested in the multivariate analysis is that the food web can be considered nested (i.e., variation at any hierarchical level within the food web is best explained by one or more predictor variables that do not interact, or do so to

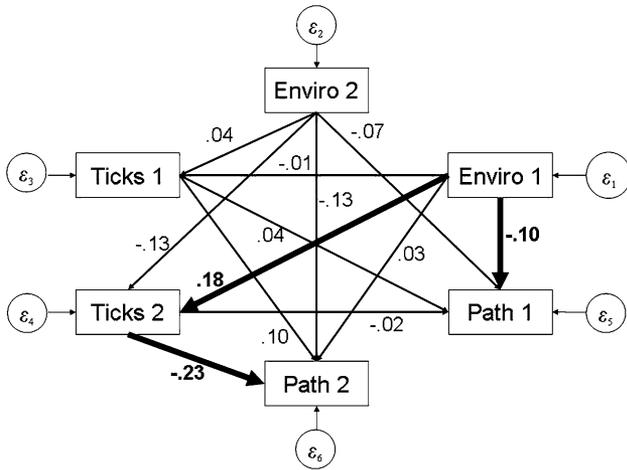


Figure 1. Directed graph showing the structural equation model of the interactions between pathogens, ticks, and the environment. The numbers indicate the first and second components obtained from Bray-Curtis ordination. Arrows show the direction of interaction; the numbers on each arrow indicate the strength of the interaction; boxes contain variables; and the circles with ϵ_i indicate normally distributed measurement errors in each variable. Numbers and arrows in boldface are significant to $P < 0.05$. The values of the six error terms ϵ_1 to ϵ_6 were 0.12, 0.05, 0.04, 0.03, 0.02, and 0.01, respectively. Further statistics for each interaction term in the model are provided in Table 1.

a lesser extent, with another web level). We tested for interaction effects between pathogen occurrences, tick occurrences, and abiotic variation using SEM on the first two orthogonal components of each data set. The basic model that we were interested in testing was the one in which the environment influences ticks, and both ticks and the environment can influence pathogens (Fig. 1 and Table 1). The model was formulated a priori as a test of our central hypothesis; although many alternative models are possible, the validity of this particular model when confronted with data was the question of greatest interest for our particular analysis. The fit of the model was significant (χ^2 5.815, d.f. 3, estimated probability that the saturated and default models are different = 0.121).

The results in Figure 1 and Table 1 show that the effect of the abiotic environment on tick community composition is strong (first abiotic component effect size on second tick component = 0.18; $P < 0.014$). The effect size of tick community composition on pathogen community composition is also significant (effect size -0.23 for tick component 2 interacting with pathogen component 2; $P < 0.009$); note that since the second component represents community-level variation not captured by the

Table 1. Partial Regression Weights from SEM, Showing Significance and Standard Errors of Interaction Terms in the Directed Graph Presented in Figure 1^a

Effect	Estimate	SE	$P <$
Ticks 1 \leftarrow Enviro 1	-0.013	0.112	0.906
Ticks 1 \leftarrow Enviro 2	0.037	0.175	0.830
Ticks 2 \leftarrow Enviro 2	-0.136	0.115	0.237
Ticks 2 \leftarrow Enviro 1	0.182	0.074	0.014
Path 2 \leftarrow Ticks 1	0.097	0.060	0.104
Path 1 \leftarrow Ticks 1	-0.043	0.063	0.499
Path 2 \leftarrow Enviro 1	0.031	0.048	0.526
Path 2 \leftarrow Enviro 2	0.017	0.071	0.806
Path 1 \leftarrow Enviro 2	-0.013	0.075	0.868
Path 1 \leftarrow Enviro 1	-0.109	0.051	0.033
Path 1 \leftarrow Ticks 2	-0.016	0.096	0.867
Path 2 \leftarrow Ticks 2	-0.238	0.091	0.009

^aIn the "Effect" column, numbers 1 and 2 indicate the first and second component from a Bray-Curtis ordination; Ticks, tick data; Enviro, abiotic data; Path, pathogens; and the arrows indicate the direction of the interaction. Column headings are as follows: Estimate, estimate of effect size; SE, standard error of effect estimate; $P <$, estimated significance (probability less than).

first component, we do not ascribe particular significance to the direction (sign) of the relationship. The interaction of the first abiotic component and the first pathogen component is weakly significant (effect size -0.1 ; $P < 0.033$). The SEM results thus confirm the patterns identified by the simpler bivariate analyses, while suggesting that there remain causes of variation in each of the tick and pathogen data sets that are not fully explained by the variables that we measured.

DISCUSSION

All of our statistical analyses yield essentially the same results: (1) that climate has a strong influence on the species richness and community composition of ticks; (2) that the tick community has a strong influence on the pathogen community; and (3) that there are significant effects of abiotic variables on pathogen species richness and community composition at a national scale, but these effects are small and are considerably weaker than those exerted by tick community composition. More specifically, the results show that the abiotic environment exerts roughly twice as large an influence on tick species richness as it does on tick-borne pathogen richness.

For this host–parasite system, the dominant interactions occur between abiotic conditions and tick diversity, and between tick diversity and pathogen diversity. Such an arrangement of food web levels in a hierarchy may be characteristic of other vector-borne diseases as well (e.g., see Krasnov et al., 2004). Since many pathogenic bacteria and viruses are highly associated with one or a few particular vector species (e.g., Wilson et al., 1990; Walker et al., 2000), there is a tendency for more diverse local vector communities to host a larger diversity of specific pathogens. However, it is less intuitive that for African tick species and associated tick-borne pathogens with a broader range of host specificity, a higher diversity of tick species apparently generates a larger diversity of generalist pathogens as well. Vector community composition has a proportionally greater effect on pathogen community composition than the converse, because pathogen life histories are more intimately tied to their hosts than to any other environment (Price, 1980).

The low but direct effect that we found of the abiotic environment on pathogen community composition is intriguing, and may be partly due to the low number of pathogen species for which data were available. Further investigation of the consequences of abiotic impacts on supposedly top-down food webs is clearly needed. There has been considerable discussion about whether climatic conditions may influence disease emergence and spread in the future (e.g., Price, 1980; Randolph and Rogers, 2000a, b; Randolph, 2001; Hay et al., 2002; Rogers and Randolph, 2003). Our results suggest that studies of the influence of the environment on vector-borne diseases need to be considered in context and across the spectrum of different spatial and organizational scales that exist in nature (Loreau et al., 2001; Zavaleta et al., 2001). In any ecological system, adaptation and stasis occur through the interaction of processes that create novelty, processes that maintain the status quo, and processes that exert selective pressure to remove organisms from the community (Levin, 1999). Without understanding these positive and negative feedbacks and the ways in which they relate to environmental change, it will be difficult to tease apart the mechanisms that determine the emergence of novel pathogens in the face of global environmental change.

The data indicate that there is a considerable amount of variation in the occurrences of both ticks and pathogens that is not directly explained by the variables that we considered in this analysis. In both tick and pathogen communities, a variety of factors may be contributing to

this variation. These include sampling effects, the community composition of host species of both parasites and pathogens, predation (e.g., the influence of oxpeckers on ticks; Bezuidenhout and Stutterheim, 1980), changes in species occurrences due to the effective use of pesticides and vaccinations, access by the human population to veterinary and medical services, and variations in host abundance and population dynamics (and hence, transmission rates). Given the many possible influences on both ticks and pathogens, the fact that we have found significant interactions at a national level suggests that the signals of interest may ultimately emerge as even stronger than our “noisy” data indicate.

Removing vector species from local communities should normally result in a decrease in the number of pathogen species, at least for those pathogens that are highly specific to one tick species. These interactions, however, occur in a context in which abiotic factors may play an important regulatory role. The influence of climate change on tick-borne pathogens will play out primarily via ticks, which in turn will influence pathogen diversity with an unknown time lag (e.g., Suss et al., 2004). Whether a pathogen species increases or decreases in abundance when a vector is removed (see LoGuidice et al., 2003 for an illustration) will also depend on the strengths of the various interactions between vectors and pathogens, and between the vectors and the resources for which they may compete. Highly specialist pathogens will probably be lost from the community if their single vector species is lost; but little is known about how more generalist pathogens will respond to host loss. We envisage that some kind of tradeoff between abundance and species richness of vectors may influence pathogen persistence, with specialist pathogens being more dependent on overall vector diversity (i.e., whether or not particular species occur) while generalist pathogens are more dependent on vector abundance (i.e., sufficiently many individuals of suitable host species will sustain the pathogen population).

There is much evidence for indirect effects in species-removal experiments in predator–prey systems (Sih et al., 1998). The conclusion that we reach from this study of a single multispecies vector–pathogen community is that indirect effects, such as those of the environment on pathogens through tick species richness and community composition, will be less important in a pathogen–vector context than direct one-way effects, such as those of the environment on ticks and ticks on pathogens. Contrary to many predator–prey systems in nature (e.g., Polis and Holt,

1992), the environment–ticks–pathogens circuit is rigid in the sense that pathogen species are hosted by tick species that are themselves supported by the habitat, but never vice versa.

The emergence of novel pathogens is a topic of high current interest in the context of global climate change and other kinds of anthropogenic modification of habitats (Daily and Ehrlich, 1996; Patz et al., 2004). From a food web perspective, pathogen emergence will be partially dependent on the dynamics of host–vector–pathogen systems and the ways in which the community composition of each trophic level acts to either create or remove novelty. The existence of diverse vector–pathogen species interactions may indicate food web stability (Pimm, 1984; Levine and D’Antonio, 1999; Ives et al., 2000) and hence a lower likelihood of the emergence of novel diseases, but further work is clearly needed here. It is also unclear whether the same patterns will occur at finer scales, or whether differences in such variables as host occurrences and behaviors will have a more significant fine-scale impact on the local dynamics of vector–pathogen interactions. In general, although our results demonstrate that host–vector–pathogen food webs may show nesting at the community level, a considerable amount of additional research will be required before the complex interactions that determine host–vector–pathogen community dynamics are fully understood.

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