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Ecological niche of plant pathogens

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Abstract. Disease ecology is a new approach to the understanding of the spread and dynamics of pathogens in natural and man-made environments. Defining and describing the ecological niche of the pathogens is one of the major tasks for ecological theory, as well as for practitioners preoccupied with the control and forecasting of established and emerging diseases. Niche theory has been periodically revised, not including in an explicit way the pathogens. However, many progresses have been achieved in niche modeling of disease spread, but few attempts were made to construct a theoretical frame for the ecological niche of pathogens. The paper is a review of the knowledge accumulated during last decades in the niche theory of pathogens and proposes an ecological approach in research. It quest for new control methods in what concerns forest plant pathogens, with a special emphasis on fungi like organisms of the genus *Phytophthora*. Species of *Phytophthora* are the most successful plant pathogens of the moment, affecting forest and agricultural systems worldwide, many of them being invasive alien organisms in many ecosystems. The hyperspace of their ecological niche is defined by hosts, environment and human interference, as main axes. To select most important variables within the hyperspace, is important for the understanding of the complex role of pathogens in the ecosystems as well as for control programs. Biotic relationships within ecosystem of host-pathogen couple are depicted by ecological network and specific metrics attached to this. The star shaped network is characterized by few high degree nodes, by short path lengths and relatively low connectivity, premises for a rapid disturbance spread.
Keywords disease ecology, pathogen fundamental niche, pathogen realized niche, ecological network of host pathogen system, model organisms, *Phytophthora* spp.

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Introduction

Pathogens are recognized as structuring force in natural communities, a fact emphasized by Clements still from 1928 (Dobson & Crawley 1994, Van der Putten & Peters 1997, Lafferty et al. 2006, 2008, Pascual & Dunne 2006).

Parasites play major roles in ecosystems: they promote diversity, as they affect the populations of dominant species. The consequence is the facilitation of subordinate species to build up larger populations. Parasitism and disease are, probably, the most significant causes of population regulation under natural control (Loreau et al. 2005). However, under environmental and anthropogenic stress, in natural and man managed ecosystems, epidemic diseases cause major economic losses and represent a major threat to biological conservation (Beldomenico & Begon 2009).

Disease ecology is a new area of study, focused on the underlying principles that influence the spatial-temporal patterns of disease (Glass 2006) and the characterization of the pathosystem in the larger context of the ecosystem. There is a need of sound theoretical frame for the understanding of complex problems concerning pathogens in ecosystems, mostly the host-pathogen interaction: such a frame is represented by niche theory.

Niche is one of the most discussed concepts in ecology, one the few theories subjected to evolution, denial and resurrection, and it is also a valuable framework for explaining how and what species become invasive (Chase 2005).

Pathogens co-evolve with their hosts, and accordingly, their niches co-vary. Generally, the species richness of parasites in various communities is underestimated, but it is hypothesized that their biomass is considerable. Plant pathogens have high ability to diversify, when new ecological opportunities appear (De Neegaard 1987). Specialization permits relatively large number of species to utilize a given resource, the hosts functioning as a system of resources.

Plants and their fungal/fungal-like pathogens are modular organisms. The potential to differentiate is greater in modular organisms than in unitary organisms (Begon et al. 2006). These categories of organisms display exploitative and exploratory strategies for resource exploitation. A compartmentalized plant is less vulnerable as an individual, to the impact of herbivory and pathogen attack (Valladares & Nümets 2007). A tree is a complex succession mosaic of hierarchically organized modular construction, which promotes heterogeneity to cope with organisms subsisting on or within it (Whitham 1981). On the other hand, fungi and fungi-like organisms combine the iterative modular growth with externalized metabolism, a way to cope with lack of mobility. *Oomycota* that includes aggressive plant pathogens (*Phytophthora* spp., *Pythium* spp., *Peronospora* spp.), form a unique branch of eukaryotic organisms, of independent yet convergent with fungi, life histories. Many pathogens display a saprotrophic life style and also attack a host or a group of host species that are members of plant communities. Accordingly, their niche is bivalent and the same controlling factors play different roles whether a pathogen infects a host or lives saprophytically. *Oomycota* display intermediate life history between sessile, iterative mode of exploring/exploiting resources and the mobile mode by means of zoospores, for pathogenic species as *Phytophthora* spp. and *Pythium* spp. meaning host acquisition. They combine filamentous growth strategies, common for real fungi (as evidence of horizontal gene capture from fungi), and microbial motile mode.

Plant pathology and epidemiology focus on pathogen-host interaction, on disease progress, on molecular mechanisms involved in disease, in order to find most efficient control methods. In forest plant pathology, much effort is consumed to early diagnosis and prevention of tree diseases in natural and managed woody ecosystems. The emerging domain of disease ecology widens the area of investigation in the frame of population, community, ecosystem and landscape ecology, by considering host-pathogen relationship in the multispecies networks of trophic and non-trophic interactions (Glass 2006).

The integration of pathogens and disease in ecosystem structure and processes is one of

important research streams, a special case deserving attention - niche description in terms of critical factors for survival of both pathogen and host.

A pragmatic approach to niche concept applied to pathogens is to consider them as an entity to be analyzed, the host - pathogen system in the environmental envelope and complex relationships build with other functional categories of organisms, at different trophic levels. At the present time, scientists have gathered knowledge on molecular interactions, characteristics at individual and population level of the interaction described by both pathogen and host attributes (epidemiology and symptomatology as pathogen-host interaction variables), on environmental factors facilitating disease and very little knowledge on interactions of pathogens with other organisms than hosts (competition, predatorism or hyperparasitism). Lately, it was recognized that pathogens can be keystone species, which control productivity and main processes in ecosystems, that in equilibrium conditions they act as density dependent controlling factors of the host populations (Manion 2003). We know little about their favorable and unfavorable ranges, with respect to environmental variables included in the niche. However, knowing the species niche characteristics one is able to explain and predict biological invasions (Dash 2007). For instance, species of genus *Phytophthora* used as models for the argumentation in the present paper are necrotrophic pathogens also invasive organisms causing epidemic development in a large number of plant species, many of them being woody species, both in natural and man managed ecosystems.

In this paper I overview the main traits of the niche theory applied to pathogens and host-pathogen systems, with special emphasis on *Phytophthora* spp. Also for the sake of argumentation I propose the new methodological approach of ecological networks, developed on a worked example, the couple *Phytophthora quercina – Quercus* spp and the associated functional groups of organisms (predators, pathogens, competitors, mutualists, facilitators) to both focal species of the couple and to each of them. It is used to analyze quantitatively and qualitatively the interspecific relationships of hosts and pathogens as main axes of the realized niches in the sense other authors stressed previously (Hannon 1973, Fath at al. 2007). ENA (ecological network analysis) is a holistic methodology permitting the study of interactions (food-web, pollinator-plant, mutualistic, etc.); the network analysis based on graph theory permits to reveal higher order properties of direct and indirect interactions figured as links connecting nodes that correspond to species, functional groups of species or other entities influential in terms of relationships such as nutrient pool or detritus (Fath 2007).

The paper is structured in parts corresponding to important issues connected to niche theory: (i) how the niche concept has evolved and which are the actual main streams, (ii) how is defined the fundamental niche and how this definition can be extended to pathogens coupled with hosts and disease, (iii) how realized niche is circumscribed in the particular case of pathosystems, (iv) how realized niche with respect to interspecific relationships can be depicted and quantified using network approach. A network organized around *Phytophthora quercina* and *Quercus* spp. is proposed to illustrate this concept.

Most effort in studying pathogens at large was directed to answer questions such as “what and how”. Niche theory answers to the question ”why” a pathogen dwells in a particular community (the presence of a pathogen is host driven but also community driven), being at the same time, a member of the pathogen subsystem or guild, and member of microbial community.

Niche theory evolution

There is a vast plethora of niche definitions, subjected to revision and reconstruction with time. The basic idea is that niche is an integrative concept. It is also an organizing principle in ecology: it summarizes the effects of opportunity and constraint of the environment, as they are used by individuals, populations, species and communities (Hannah & Freeman 1993). It is also a system concept because it addresses how ecological objects fit together to form wholes/entities (Patten & Auble 1981). Niche contains sets of biotic and abiotic conditions of the environment that define the limits of a species ability to survive. Alternatively, the niche is a set of resources occupied by an organism (Putman & Wratte 1984). Early approaches of Grinnell and Elton emphasized the niche as species habitat requirements and the fact that niche is a property of the biotic community. Later niche formalization, the niche hypervolume introduced the concept of niche variables and axes. Each dimension of the hypevolume is a variable and variables are interrelated to match species to environmental gradients (van der Maarel 2005). This new approach lead to the opinion that environment contains empty niches waiting to be filled (Reich et al. 2003). The principal trigger of niche differentiation is the competition and species can co-exist as a consequence of this differentiation (Hutchinson 1959, Tilman 1985)

The classical, hutchinsonian approach of the fundamental and realized niche, is still the most operational. Niche space contains several distinct regions summarized in various ways as for example: habitat, trophic and multidimensional (Dash 2007).

The basic idea is that there are several important axes to be considered, those which correlate best with species survival. An example is soil pH and concentration in nitrate ions, as best predictors for the presence of arbuscular mycorrhizae (Fitzsimons at al. 2008).

Organisms also alter the environmental variables, an aspect that has been included in the niche concept (Chase & Liebold 2003).

In a similar manner with individual, population and species niche, a community niche can be defined as the total niche space being a multidimensional volume in which different species exist, with each dimension representing a particular resource or abiotic gradient (Keeney & Poulin 2007). Parasitic communities are described with respect not only to species composition but also to functional richness, each species occupying a specific niche space, for instance a specific organ or host tissue. Within each functional group, species redundancy is expressed by same traits, in a more pronounced manner at closely related species. Species which share a large number of biological traits also experience wide niche overlap (Hérault et al. 2008).

One of the most debated issues in niche theory was generated by the statement of the preexistence of niches or empty/vacant niches (Lewontin 1978, Rohde 1991) versus the niche as an individual/population/species property (Chase & Liebold 2003). Rohde (1991, 2005) has shown that hosts are preexisting niches for parasites. A proof of the statement is the fact that invasive species, initially enemy-free, acquire parasites in time. As a general rule, hosts are not saturated with parasites (Lekevičius 2009). It is a partial explanation for the colonization success of alien *Phythophthora* species, which are also highly competitive and can displace the resident pathogens.

Niche concept centered on species requirements and functional position is a lucrative frame for other important theories and concepts in ecology: distribution of species abundances and diversity, community structure and trophic web (MacArthur 1960, Pielou 1975, He & Tang 2007).

The hyperspace concept made niche more affordable in practical, quantitative terms (Strain & Billings 1974). This hyperspace can be divided in subspaces, containing sets of conditions or variables to be analyzed. In other

words, niche space is a set of environmental variables and all the response vectors of the organism. Niches can be modeled: environmental variables can be measured along axes, and internal structure of the niche is determined by the species performance (population fitness) (Petersen 2007). Response variables are niche dimensions, depicting the reaction of populations/species. Species abundance is a response variable, included in the niche preemption model. Most abundant species acquire the most important part of a particular resource, a model which describes communities with few dominant species (He & Tang 2007).

In plant-pathogen interaction, there are genomic responses of the plant to infection (Straalen & Roelof 2006), which can be quantified. Any point inside this space is a function of all environmental variables and responses. If there are overlaps in environmental vectors (or trophic vectors) of two organisms, a competition region differentiates. Niche can be summarized as a system of stochastic/deterministic, compartment or static/dynamic models, there are internal and external variables included in models, but for the time being most of the models treat external variables. Adjacency matrices and ecological networks are used to depict possible links between state variables, such as vegetation, climate, hosts and disturbance regime. Niche modeling is another promising direction in niche description comprising abiotic niche including disturbance regimes, biotic niche and accessibility within dispersal capabilities. The later is not a niche dimension, but a set of factors that constrain the species to inhabit less than its distributional capabilities. The geographical projection of these conditions represents the distribution of species (Peterson 2006). In the case of pathogens, I consider that proxis for population parameters are pathogenicity, virulence, infectivity, or disease attributes, such as disease severity or disease frequency and they can be used for the construction of matrices. These are functional traits that are directly or indirectly measurable. It is a valid approach in quantifying species niche by using traits instead of environmental parameters (Violle & Jiang 2009). In fact, the niche may be also defined as a fitness measure in a multidimensional environmental space (Levins 1966, Holt 1987).

Intersection niche of host and pathogens

Host and pathogens share axes of the environmental envelope, which encompasses also the space of the fundamental niche. Because of the principle of competitive exclusion, species are placed in different positions along same axes that eventually represent several environmental gradients.

The most striking difference between the ecology of parasites/pathogens and free living organisms is the fact that the habitat of the pathogen is a living organism (Begon et al. 2006). Host plays the role of habitat and nutrient resource for the pathogen, meaning that host contains axes of the fundamental niche related to habitat and to resources for the pathogen, as well as axes representing utilization or physiological response of the pathogen. Realized niche of the pathogen incorporates response of the hosts to infection as well as biotic limiting interactions discussed in more detail further in the text. The outcome of parasitic relationship is controlled by the host physiology at individual level and the degree of individual traits variability at population level. The niche of a pathogen with complex life cycle, including host alternation or saprophytic stage, is adjusting, changing and it is affected by biotic and abiotic environment, within the limits of its genotype and phenotypic plasticity.

The interaction of the host with the pathogen places pathogen attributes among the axes of the realized niche. Also, the niche not being a property of the species, it shows variation between populations. In terms of popula-

tion attributes or pathogenic markers, different pathogen populations display different virulence or infectivity. An alternative approach is consid to host defined ecological niche of a pathogen or group of pathogens (Gudelj et al. 2004), which means a host imagined as a partial niche hypervolume for the pathogen. Pathogen-host interaction have two outcomes: (1) same pathogen – new host, (2) emergence of a new pathogen, in both events the niche being re-dimensioned. One largely commented example is of the emergence of *P. alni,* causing alders' decline in Europe, from *P. cambivora x P. fragariae* by means of hybridization (Brasier 1999).

There are two major approaches in niche description: (i) structural, which takes into account the trophic relationship host-pathogen, population structure with specific attributes of the pathogen (virulence, pathogenicity, infectiveness) of the host (resistance, anatomical, physiological barriers), the habitat description including environmental envelope and relationships with other organisms and (ii) functional, with three hierarchical levels: molecular (gene-to-gene, elicitors), individual (which is a physiological response) and population (numerical response in terms of host fitness, host biomass as consequence of host-pathogen interaction and the numerical response of the pathogen in terms of populations of lesions).

An important issue related to host-pathogen interaction is the body scaling: there are scale differences between host and parasite, while body size predicts the metabolic rate, energy uptake, physical forces have different impacts on small organisms (pathogens), as compared to large organisms (hosts) (van Straalen & Roelof 2003).

It is worth to mention that niche dimension of the patho-system is different during epidemics to the same from the latent development of pathogen population. Pathogens attacking same organ or tissue are grouped functionally in guilds. Members of the guild share at least three important axes: resource, namely the host organ/tissue, space or location inside host and host response to infection (Pedersen & Fenton 2006). These axes are placed in different places: host niche, disease niche, pathogen niche.

The dynamics of infectious disease is viewed as an overlap in time-space of niches, of the component populations (Glass 2006). In the case of vectored diseases, there is an overlap

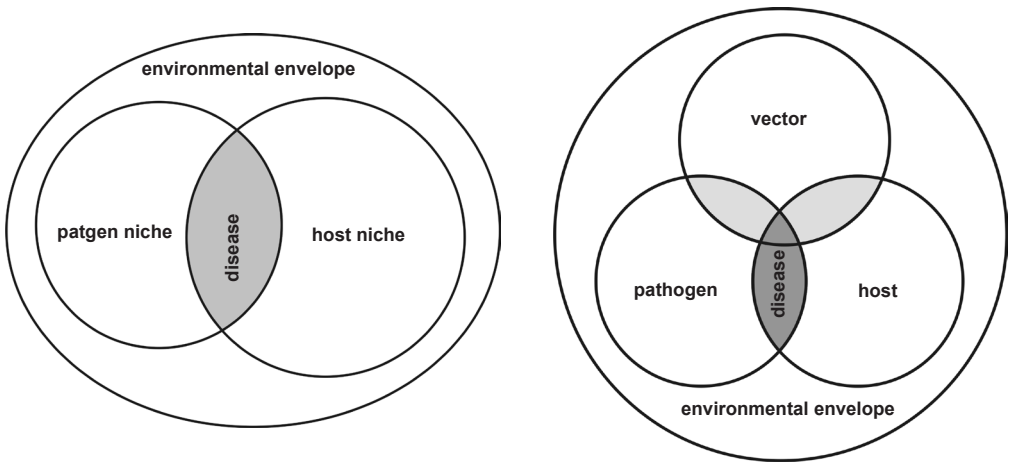

Figure 1 Intersection of host, pathogen (left) and host-pathogen-vector (right) niche within the environmental envelope diagram.

among pathogen niche, host niche and vector niche (Fig. 1).

An intriguing issue is the virulence, as an important trait, which can be severe, with lethal outcome, sustaining the paradox of the pathogen that both harms and depends on the host (Dethlefsen et al. 2006). The common view is that virulent pathogens originated recently and had not established a balanced relationship with the host. The measure of pathogens performance represents the reproductive output and the transmission success, meaning that the host must survive long enough to permit the reproduction and dispersal of the pathogens. The selective trade off in the case of many epidemic *Phytophthora* species is directed in maximizing the production of infectious propagula before the host succumbs. However, an optimally virulent pathogen is possible to be a poor competitor in mixed infections.

Virulence together with other pathogen attributes (infectivity, pathogenicity) describes pathogen population and represents response variable in niche space. Increase of virulence appears when a pathogen invades a new environment, host or tissue and is the general case of emerging or invasive pathogens such as *Phytophthora spp*. In fact, up to 65-85% of pathogens in a region are alien (Pimentel et al. 2000). Most of *Phytophthora* spp. being invasive species, the mechanism of extra-range dispersion is poorly understood. For the moment, one single explanation covers the known introductions: human trade.

Lesions form distinct populations and represent a measure of disease severity (response variable) as well as of potential transmission success. For instance, in the case of infected host with *Phytophthora ramorum* a significant relationship was described between lesion area on leaves and the number of resting spores suggesting that more inoculum is produced from larger lesions (Anacker et al. 2007).

In my opinion, host disease related traits such as susceptibility are important axes that can be placed in the intersection area corresponding to disease.

Fundamental niche of the pathogen

Fundamental niche is an abstract construction. It contains axes connected to host as habitat and resource but also to environmental envelope that affect both partners in a different way or in different regions along axes representing environmental gradients. At large scales, climatic envelope that incorporates most important abiotic axes, dictates the species distribution.

I consider that disease intersection describes the space of the hypervolume which incorporates the successful acquisition of the host resources by the pathogen, the favorable (for the pathogen) regions of the environmental gradients, and successful colonization of the habitat, namely the host. For the sake of symmetry, same axes incorporate for the host the unfavorable regions along environmental gradients facilitating the pathogen. For instance, soil prolonged flooding which is a limiting condition for trees and is a favorable condition for soil-borne species of *Phytophthora*.

A subsystem of fundamental niche is the habitat of a species (habitat niche), population or community, for pathogens, a part of the habitat is the host itself. Niche of an organism can vary although the habitat is the same.

If there are no habitat vectors in common, no niche overlap occurs. Overlap appears in the competition region. Response vectors differ in different parts of a species niche as biological processes respond to environmental gradients. There is an optimal part of species niche and suboptimal in other areas.

In my opinion, the habitat of pathogens scales at least at three levels: the restricted habitat is represented by the host, sometimes a particular tissue or particular organ; the extended habitat is represented by the microenvironment close to the host and the general population habitat. The restricted habitat is defined by molecular interactions and incorporates axes of the fundamental niche as well as axes of realized niche

since pathogen-host interaction is a particular type of biotic relation. The extended habitat contains axes of the fundamental niche. The habitat of pathogens represented by the host is also a nested entity consisting of target tissue, target plant species, target population within a target community, within a specific ecosystem within a specific landscape. Habitat use is also nested: biochemical regulation of pathogen-host interaction, susceptible individuals within population and the process of probabilistic/stochastic interception by pathogen meaning successful colonization and successful dispersal with respect to community and ecosystem, also influenced by some landscape attributes such as connectivity, topography, and spatial distribution of environmental factors relevant to the hosts.

Habitat alteration increases disease risk, a fact sustained by extended crisis phenomena affecting habitats worldwide. Environmental disturbance increases the rate of evolution of fungal pathogens. Hybrids have increased aggressiveness as the case of the newly emerged pathogen, as *Phytophthora alni* demonstrates (Brasier et al. 1999). Asexual reproduction and self fertilization commonly encountered in many species of fungi and fungi-like organisms are beneficial for marginal populations in marginal habitats.

At regional and continental scales, biogeographic processes that affect hosts must have some influence on the pathogen. For invasive pathogens which is the case of *Phytophthora* spp. there are several probabilistic filters contributing to the establishment in new area and/or host: local habitat suitability in terms of abiotic factors between the accepted limits of variation for the pathogen (climatic factors are highly correlated with pathogens), susceptible host, colonization capacity, sustainability of a viable population (Møller 2005). Predictive models of *Phytophthora* potential occurrence at large, regional scale were generated using detailed climatic data and temperature requirements inferred from laboratory trials. One example is CLIMEX model for potential establishment of *Phytophthora ramorum* in Eastern United States (Venette 2005). This model resulted in being sensitive to parameters describing pathogen's response to heat stress and initial moisture promoting growth. However, the assumption that laboratory trials are reliable and can be extrapolated to field conditions is risky.

The fundamental niche of an organism can be entirely contained in the fundamental niche of another organism (a frequent case in host associated microbial communities), more often niches overlap which is a measure of association between organisms. We can predict the niche evolution from the knowledge of the environment and resource utilization of each species. For instance, abiotic factors requirements are differential and permit a temporal, spatial as well tissue type succession of pathogens (niche package): *P. syringae* has optimal temperature at 20° C and is found to be active on woody tissue during dormant period. *P. citricola* and *P. cactorum* have optimum at 25-28° C and are found on sprouts during the spring. In case of *P. ramorum* relevant field variables at biogeographical scale are: minimum average temperature, mean precipitation, longitude. Each species has a particular and optimal combination of factors at which performs best, leading at the community level at niche differentiation. On the other hand each species covers only a part of the habitat considered as being optimal (Tilman 1999). Suboptimal habitats are occupied as a consequence of competition pressure, with a weaker species performance. The tree genetic variability is overridden by effects of local environmental factors at landscape level (Anacker et al. 2007) explaining the way it performs when confronted with pathogens.

To understand niche, not only limits must be known but also the level of response within limits. It is sufficient to describe several critical variables corresponding to a partial niche (Maguire 1967) which determine the survival. Such partial niches are (Terradas et al. 2009): resource niche, habitat niche, life history niche, fluctuation niche (heterogeneity of the niche

determined by environmental fluctuations – incorporates in the niche model the disturbances as influential shaping factors).

In my view, there is an important issue in niche subspaces identification: existence of specific host variables, pathogen variables and specific disease variables such as disease frequency and severity.

To the fundamental niche is related the dispersal of the pathogens. Biotic vectors are covering a gradient from facilitation to mutualism in relation to pathogens and there is a sub-region of intersection of pathogen and host fundamental niches.

Colony growth characteristics, used for species description, are indirect niche specifications, namely of fundamental niche, corresponding to physiological requirements of the organisms. For instance, there are differences in growth rates, depending on media. *Phytophthora polonica* displays moderately-slow growth on CA (carrot-agar) and CMA (corn meal agar) at 20º C and slow on PDA (potato-dextrose-agar) and MEA (malt extract agar) (Belbahri et al. 2006).

During its life cycle, *Phytophthora* spp. responds in two ways to resource pool, which is spatially scaled and, accordingly, varies its performances on different resources: (i) during saprotrophic stage - fine grained, localized resources, litter and soil, (ii) during pathogenic stage - coarse grained, more dispersed resources (Ritchie & Ollf 1999, Chase 2005), namely the hosts.

Soil borne pathogens have a restricted mode of dispersion and several types of vectors are involved, that justify the rapid spread of *Phytophthora* spp. as invasive organism in the world.

In connection with disease niche, the concept of ecosystem vulnerability is an important starting point in predictions regarding species and ecosystems are possible targets to invading pathogens. Vulnerable ecosystems to *Phytophthora spp*. are riparian ecosystems; clade 6 of *Phytophthora* is associated with riparian ecosystems or forest soils. Diseases develop under highly favorable conditions (Brasier et al. 2003) meaning that saprophytism is expressed in suboptimal conditions, while parasitism requires highly favorable conditions; an environmental gradient is paralleled by saprotrophic-parasitic gradient. Ecological strategies of *Phytophthora* are: adaptation to aquatic environment, ability to use organic debris, pathosystems which evolve to the attack a wide range of woody perennials.

Important fundamental niche dimensions can be simulated during the cultivation of pathogens on media. However, combination of suboptimal factors, which cause cessation of fungal growth in culture, is a poor predictor of effects in nature where competitive interactions occur (Deacon 1997). Organisms with different life styles (saprotrophic and pathogenic) have two different niche configurations which intersect. The criteria used to assess medium favorability in terms of niche axes/resources are the medium on which the organism reproduces. Suboptimal medium induce reproduction and act as limitative factors (Nielsen et al. 2007). However, the results cannot be extrapolated in nature, where many other variables shape the niche of the pathogens.

The incorporation of metapopulation theory (Hanski 1998) in niche model brought new insights in the structure of the fundamental niche. With regard to pathogens displaying saprophytic/pathogenic life style, saprophytic substrates, for *Phytophthora* those being confined to decomposing litter in soil or in water are sink habitats while the host represents the source-habitat. Sink habitats extend in fact the fundamental niche.

Realized niche of host-pathogen system and ecological network model

A full understanding of symbiotic associations, such as parasitism, requires examining the direct and indirect interaction of parasites

and the ecological community within which they evolve. Indirect interactions can influence the outcome of parasitic relationship (Suen et al. 2007)

Niche concept provides instructive context, when it is used to evaluate species interaction (Chase & Liebold 2003). Moreover, network patterns are assumed to represent niche properties, when drawing conclusions about dependencies on certain association partner (Menzel & Blűthgen 2006). Plant community structure influences the community of pathogens, while plant species richness and composition influence the spread of pathogens. The effects of invasive pathogens on community structure, as depicted also by ecological networks, is not entirely explored (Desprez-Loustreau et al. 2007), being one of the major areas of interest in the future. Trees are hosts for numerous pathogens being in fact, a complex niche with many subspaces, some of them vacant or at a particular time window, pathogen free.

Most important interspecific interactions that shape the realized niche are the trophic interactions, linked in the food web. Apparently, parasites dominate the food webs (Lafferty et al. 2006). The specificity of parasites for hosts is greater than predator-prey specificity, and the interaction implies more of the hypervolume space in terms of variables, of which many are contained in the fundamental niche and the rest in the realized niche. Little interest was directed toward interspecific interaction, other than host-pathogen, taking into account that the pathogens can occupy the position of top consumers in the food webs, but they also interact with species at different trophic levels (Desprez-Lousteau et al. 2007). The construction of the ecological networks, incorporating host-pathogen interaction as focal nodes, reveals community modules as multispecies extensions of pair-wise interactions as well as indirect interactions. Knowledge about the structure of a network sheds light on important issues, as community functioning, stability, important axes of the realized niche of some focal interest species, prediction of the response to disturbance.

Ecological networks in the study of host-pathogen interaction

In the following section I propose a theoretical ecological network of relationships describing the links between different types of organisms, from different trophic levels, with whom the focal organism, *Phytophthora quercina,* is supposed to interact, either directly or indirectly. The considered functional groups, organisms of direct and indirect interaction, were: host the most important trophic link to the pathogen, host related interactions, all being indirect links, with respect to the pathogen, such as predators (phytophagous insects), competitors, mutualists, facilitators and pathogen related links with its own predators, competitors, hyperparasites, mutualists and facilitators. The proposed network was generated for illustrative purpose, nodes representing functional groups of organisms interacting with the focal pathogen and links - the antagonistic or mutualistic interactions. Originally, this type of representation was used for food webs being based on graph theory (Cohen 1978, Pimm 1982), but I extended the network beyond trophic relations, in order to understand at a general level, the complexity of relationships established around host-pathogen interaction. The nodes (functional types of organisms) and links are appropriate heuristic approaches to describe the realized niche of *Phytophthora quercina,* considering the host defined niche (the host - *Quercus* spp.). The links connecting groups of species are, in fact, constraints imposed on niche space of host and of the pathogen. Looking at sub-graphs (interactions with a particular functional group) and to the entire network structure, one can understand where the are weak points, in terms of actual knowledge and where more research effort is needed, with the ultimate goal of disease control and

A network/graph is defined as a set of vertices connected by a set of links or edges. An edge is a line emanating from a vertex i to the vertex j. Examples of networks are Internet, chemicals connected within metabolic pathways, human social relationships, trophic webs, etc.
Node degree D_i is the number of edges per vertex. Distance d_i is the number of edges connecting two vertices. Connectivity or connectance is a global net index and quantifies the realized number of links per network (V - total number of vertices, L for total number of observed links), being a measure of network complexity:

$$C=1/2[L/V(V-1)]$$

Centrality measures: betweenness of a vertex *i* is a number of shortest paths between pairs of other vertices that run through the vertex *i*. An average network betweenness centrality can be calculated:

$$B_i = \sum_{j \succ i} \frac{g_j k_{(i)} / g_i k}{(n-1)(n-2)}$$

$g_j k$ is the number of equally shortest paths between vertices *j* and *k*, $g_j k_{(i)}$ stands for the number of these shortest paths that include vertex *i*.
Centrality measure, closeness centrality measures how close to a focal vertex is to all other vertices in the network.

$$C_i = \sum_{j=1, i \neq j} \frac{d_j}{n-1}$$

A path is a sequence of adjacent edges, without traversing any vertex twice. Average path length (distance) is the average of shortest paths between all nodes in the network. As principle, networks are characterized by short path ,no matter of how many vertices and links they display, a property called small world effect (Albert & Barabási, 2002).
Network diameter is the maximal distance between any pair of its vertices and it is a measure of the cohesion of the network.
The complexity index bi is the ratio of the vertex degree ai and its distance degree di. The sum over all *b* indices in the network is the complexity index *B* which is a convenient measure of network complexity:

$$B = \sum_{i=1}^{v} \frac{a_i}{d_i}$$

Box 1 Network metrics employed to illustrate the host-pathogen system and its biotic interactions

biodiversity conservation.

The choice was made according to the current opinion that oak decline in Europe is determined in high degree by *Phytophthora* induced diseases (Jung et al. 1999). *P. quercina* was the most frequently isolated species from oaks in Central Europe, displaying the highest plasticity concerning geological substrate and soil pH (Jung et al. 2000), being soil borne pathogen. Together with *P. cambivora,* were demonstrated as the most aggressive species of the group toward roots of young seedlings of *Quercus robur*, in soil tests (Jung et al. 1996, Jung et al. 1999, Jung et al. 2000). The ecological network representation, which is opened also for the inclusion of abiotic variables as nodes, is a promising theoretical, as well as pest control approach leading to multitarget strategies (Andras et al. 2007). More detailed information on the significance of nodes is provided based on

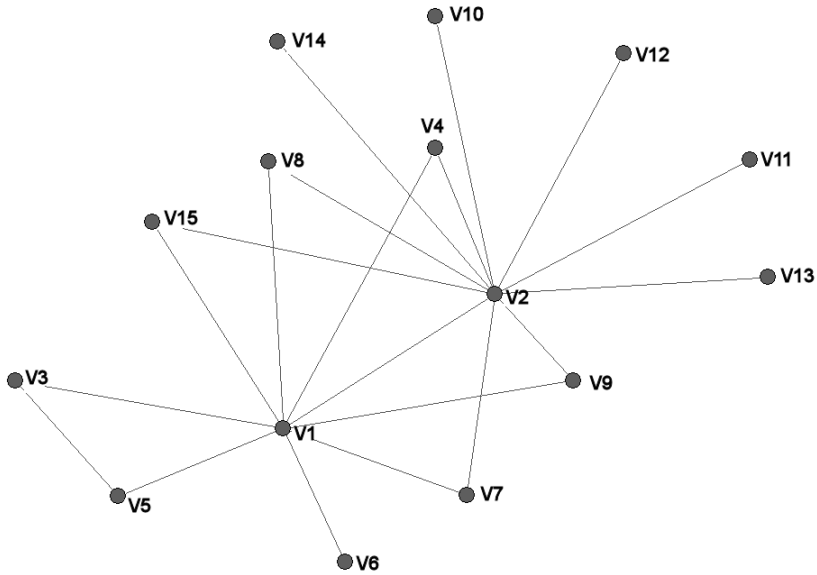

Figure 2 Graph of biotic relations of host-pathogen interaction, *Quercus* spp. and *Phytophthora quercina* model

Notation: vertex1 - host tree; v2 - focal pathogen; v3 - predation by herbivores on host tree; v4 - mycorrhizae; v5 - endophytic mutualists; v6 - non-competing with focal pathogen group of tree pathogens; v7 - trees intraspecific competition; trees; v8 - interspecific competition ; v9 - facilitators of the hosts; v10 - predators on *Phytophthora*; v11 - possible mutualists of *Phytophthora*; v12 - Hyperparasites of *Phytophthora*; v13 - saprophytic competitors of *Phytophthora*; v14 - pathogenic competitors; v15 - *Phytophthora* facilitators. The network was generated using Pajek software (Batagelj & Mrvar 2010)

references in order to clearly depict de nature of relationships (Table 2).

Figure 2 depicts the network of main biotic relations of the host, *Quercus* spp. and *Phytophthora quercina*, the link between those two partners being the focal link with respect to all links in the graph. Nodes or vertices represent functional groups of organisms linked to the subsystem established by host and pathogen. A pathogen can be regarded as nodal attribute of the host (Chen et al. 2008) and reciprocally. For simplicity the graph is undirected and no particular weight is assigned to any link. Links can be seen as axes of the realized niche of both partners of the "pathosystem". Associated metrics which describe graph topology, also descriptors of the niche axes, as presented in Table 1.

There are two distinct sub-graphs: one related to the host, and the other to the pathogen. Most of the links of the pathogen sub-graph are soil related, being integrated in detrital food webs. Any perturbation in this sub-graph (addition of pesticides, for instance) will trigger the decline of organisms placed in different nodes, with possible enhancing effects on the pathogen (predators of the pathogens, hyperparasites, saprophytic or pathogenic competitors nodes removal), during its saprophytic stage, or at the beginning of the infection process.

Host is also linked to the number of aboveground and belowground functional groups, with positive (mutualists, facilitators) and

Table 1 Network metrics of *Quercus* spp. – *Phytophthora quercina* ecological network

Metrics	Network
Average degree	2.466
Maximum degree	11.000
Minimum degree	1.000
Connectivity	0.299
Network diameter	3.000
Average distance of reachable pairs	1.952
All closeness centrality	0.656
Beetwenness centrality	0.627
Complexity index B	1.690

negative links (herbivores, interspecific and intraspecific competitors). The main characteristic of the sub-graphs the existence of many isolated nodes generating tree-like structure, is a fact which is the consequence of our lack of knowledge on the possible interactions between functional groups, represented by these nodes.

The depicted network is characterized by a low network diameter a property associated with "small world effect" (Albert & Barabási 2002), low connectivity (there are only 29% realized links compared to possible links), the presence of 5 cycles, short paths between vertices, high average betweenness and closeness centrality suggesting a highly centralized network dominated by few nodes (pathogen node, host node, mycorrhizae node) and many low degree, peripheral nodes. This is a typical case of centralized, star like networks in which a disturbance spreads fast (Ings et al. 2009). Most connected vertices (the pathogen and the host), represent also keystone species. The network resulted from of the emergence of the two subgraphs (host centered and pathogen centered), with several interconnecting links. Highest node degree (11 in *Phytophthora quercina* and 8 in *Quercus* spp.) is associated with both focal organisms and there are more species grouped within functional nodes that are connected to few other species, a pattern generally encountered in nature (Montoya et al. 2006). Complexity index *B* is describing the topology, close to star, like a network with one or two central vertices of high degree and other terminal vertices of low degree, mostly 1 or 2 (Bonchev & Buck 2005). In this context, it is worth to mention that networks are dynamic, changing over time, and the number of nodes and links is fluctuating. The removal of high degree, highly connected via direct and indirect links nodes leads to network disconnection (for instance, mycorrhizae can be removed by stressful events as soil pollution, addition of pesticides): because of high average betweenness, many nodes lie on important path, connecting indirectly important nodes. It is worth to mention in this context that indirect relationships play important community roles as in the case of *Quercus* spp. herbivores on *Phytophthora quercina.*

The graph is opened, also, to extensions due to peripheral nodes: herbivores feeding on host tree are linked to other functional groups, when they are considered as focal node their predators, pathogens, parasitoids, hyperparasites, and competitors. Interplay of the positive and negative relations influence the outcome of host consumption and, indirectly, its fate if focal pathogen is encountered. Same extension can be made for the rest of the nodes, discovering new possible indirect weakly influential relations to host/pathogen interaction.

Not presented here are the interactions between affected host and categories of organisms, for whom the tree is shelter or hunting ground, commensal organisms who are expected to be influenced by the decline of the

Table 2 Relationships depicted by the host-pathogen network with respect to selected vertices

Vertex	Relationships	References
1 &2	Plants are subjected to multiple herbivore and parasite attack, the combined effect being under certain circumstances additive and under others synergistic or antagonistic as co-attack of *Carica papaya* by the mite *Calacarus flagellatus* and the pathogen *Oidium caricae* . When primary attack is developed by herbivores as defoliating insects, secondary attack in temporal succession is caused by *Erysiphe alphitoides* on many *Quercus* spp., in this case, **facilitation** being involved. Specific resistance is gene-for-gene model with concomitant presence of avirulence gene in pathogen and resistance gene in host- multiple layers of gene-for-gene interaction form the initial defense barrier against *Phytophthora* spp.in non host plants. Considering nodes as diseased individuals and links as infection events, an epidemiological network results .	Fournier et al., 2006 Kamoun, 2001 Jeger et al., 2007
3	**Predation on host**, is represented by rich communities of phytophagous insects. Predation is supposed to facilitate under many circumstances pathogenic attack by lowering the host fitness. Pathogens affect trophic structure of the biocoenosis: in the case of *Castanea dentata* extinction due to *Cryphonectria parasitica*, seven moth species dependent on *Castanea dentata* disappeared. Also insect populations outbreaks cause fitness loss of the hosts and facilitate pathogen attack.	Laferty et al., 2007
4	**Mycorrhizae** protect plants against soil borne pathogens by interference competition, occupying potential infection sites of the metabolically active roots. Among other mechanisms are competition for colonization sites and nutrients, induction of plant resistance mechanisms.	Whipps, 1997
5	**Endophytes** as tree mutualists are highly protective against *Phytophthora* species. One potential competitor for oak pathogens is the leaf endophyte *Discula quercina*. Data show that *Pythium* spp. and *Phytophthora* spp. are strong competitors with endophytic fungi for niches within plants. The status of endophytic fungi in woody perennials can be complex and labile from mutualistic to pathogenic. There is growing evidence that tree endophytes, pathogens and herbivores display a large array of interactions from mutual tolerance and encouragement to antagonism.	Arnold et al., 2003 Morrica & Ragazzi, 2008 Valois at al., 1996 Saikkonen, 2007
6	**Non-competing pathogens** such as leaf local pathogens theoretically interfere with *Phytophthora* but at the time, there no available data on this type of interaction.	
7 & 8	Competition (intraspecific and interspecific) shapes the niche of the host, is a major force in natural plant communities. Interspecific competition drives the niche diversification. Parasites alter the outcome of interspecific competition of the host population).	Alexander & Holt, 1998 Lafferty et al., 2006
9 &15	**Facilitation** was a neglected type of interaction, reconsidered in the frame of ecological theory and niche concept, it contributes to the expansion of the realized niche of the species *Allium ursinum* which is characteristic for beech and mixed beech forests in Central Europe has moderate antifungal properties and powerful antimicrobial effects**. Pathogen facilitators** are many biotic vectors those which are not mutualistic.	Bruno et al., 2003 Beldie & Chiriță, 1972 Ellenberg, 1988
10	**Predation on pathogens** is observed in many instances being one of the axes for pathogen realized niche, a consequence of the integration of the necrotrophic pathogens in detritic food-webs during saprotrophic stage. Microarthopods control the distribution and abundance of fungi in soil, some of them grazing on fungal pathogens.	Lussenhop, 1992

Table 2 (continuation)

Vertex	Relationships	References
	Sporangia of *Phytophthora capsici* and *P.nicotianae* are ingested by seashore fleas and excreted as non-viable propagules while the ingestion of the same species sporangia by snails is followed by the excretion of viable propagules.	
	Caloglyphus sp.(Acari) feeds on *Pythium myriophilum*	
	In my observations, oribatid mites which are common leaf litter dwellers, feed eagerly on *Phytophthora* laboratory cultures.	Lussenhop 1992
	It is considered that animal-fungal/ Oomycota interactions including predation, contribute to long range dispersal of propagules in food-webs.	Hydes at al. 2009
11	**Mutualists** of *Phytophthora* are highly probable to exist. No available information on this topic exists.	
12	**Hyperparasites** control populations of pathogens being important targets in pathogen control research. *Phytophthora capsici* oospores are parasitized by actinomycetes and fungal species as *Acremonium spp., Humicola fuscoatra, Verticillium chlamydosporium*.	(Sutherland & Papavizas 2008
13 & 14	Parasites are exposed to **interspecific competition** and the outcome depends greatly on their relatedness. Parasites compete for susceptible hosts at two levels of organization: within individual host and between hosts. Pathogens either occupy different niches within the host, either are antagonistic Species of *Quercus* spp. are attacked by several *Phytophthora* species, which can be isolated from soil and rhizosphere concomitantly, such as *P. cinammomi, P. citricola, P. europaea, P. cambivora, P. cactorum*, *P. gonapoyides, P. undulata* and *P. quercina*, but aside competition, in several occasions, the hypothesis of niche complementarity or other competition reducing mechanisms are alternative explanations for species co-existence .	Koskella et al. 2006 Peterson & Campbell 2002 Jung at al. 1999 Balci et al. 2007
	Particular types of competition such as antibiosis (remote interaction) characterizing microbial interaction is used as control tool as for instance, actynomycetes against species of *Phytophthora.*	Balci et al. 2008 Begon et al. 2006
	Most systemic fungi with specific niche in nature, produce mycotoxins such as antibiotics, signaling agents or mutagenic agents. *Bacillus mycoides, Renibacterium salmoninarum* and *Streptomyces pneumoniae* orientate to active roots being attracted by same compounds as *Phytophthora cinnamomi.*	Valois et al. 1996 Ciegler 2007
	For pathogens with different life styles during life cycle (saprophytic and parasitic) competition is directed against other pathogens within host, or againt other saprophytic species, in the case of *Phytophthora* with soil fungi and aquatic decomposing fungi.	Yin et al. 2004
	Within host competition selection goes on more virulent strains However, the competition outcome tested *in vitro* differs from competition observed *in situ* accordingly, extrapolation of laboratory experiments into the field is quite risky. Competition in soil takes place between soil inhabiting saprotrophic organisms and pathogens such as *Pythium* and *Phytophthora* primarily for colonization of roots and seeds and secondarily for organic matter resource acquisition during the saprophytic stage in the life cycle of pathogens. The host can be also partitioned in different sub-niches attacked by specialized pathogens (roots, leaves, bark or other plant organs as well as different types of tissue). The species separate on a particular axis but probably overlap on other axes, since competition does not affect all axes.	Koskellla et al. 2006 Fujar et al. 2005

tree, they also can be integrated as axes of the realized niche of the host, and indirect links to the pathogen. For instance, at larger scale, the destruction caused by *Phytophthora cinnamomi* in Australia has triggered the extinction of many endangered, species depending on the affected plant host species for shelter (Vear & Dell 2004)

In oversimplified ecosystems, such as managed (agro-systems, tree plantations and orchards), ecological networks are also simplified and pathogens/pests exert a top-down control, comparable to top predators.

Conclusion

Niche concept, which is an integrative one, is proposed to be used as a tool in identifying the most important variables of the pathogen, pathogen-host hyperspace: axes of the fundamental niche, response variables or ecological networks, constructed on multispecies interactions, which may become important in the ecological management and control programs. A review centered on host-pathogen system, largely neglected in ecological literature was elaborated referring to an empirical model, the system of *Quercus* spp. and *Phytophthora quercina,* representative for invasive diseases phenomenon.

Disease as a "pathosystem" component is a niche subspace, which includes axes, corresponding to gradients of abiotic factors along which optimal intervals for the pathogen, frequently corresponding to limiting factors for the host. Hosts act as acquired resources and habitats, while disease sub-niche response axes include population of lesions, symptoms, epidemic spread outcomes such as recovery or death.

Fundamental niche of the pathogen cover abiotic conditions, which are useful axes, in terms of niche modeling, also those axes are connected to the host and correspond to the restricted habitat of the pathogen. Niche modeling permits to make inferences about invasive spread of non-native pathogens, such as *Phytophthora* spp.

As parts of the fundamental niche are reciprocally included in pathogen, host and vector niche, discovering most important axes and limiting intervals is an important goal in the understanding of host-pathogen interaction. Cultivating under laboratory conditions is not always the best way for obtaining valuable information on pathogen requirements in natural environment.

Realized niche of the pathogen incorporates axes pertaining to the host, as well as axes or links pertaining to other groups of organisms if ecological network modeling is employed. The present paper is a first attempt in using networks to depict the complex structure of host-pathogen interaction, together with other beneficial or suppressive partners. The relationships depicted by networks are trophic, but also non-trophic, such as competition or facilitation. The inspection of the network suggests future directions of research on indirect relationships, which can be exploited at the benefit of the host (hyperparasites, allelopathic plants suppressive to soil pathogens, etc.)

Specific graph metrics are shedding light on species or group of species importance, also on the consequences of eliminating vertices and subsequent links. Disturbances propagate along links in the network to remote vertices affecting large groups of organisms not only the primary target of the disturbance. This is also a warning, in what concerns control methods, currently employed against tree pathogens, which are insufficiently tested in the larger context of ecological network established around pathogen-host interaction.

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