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Epidemiology

Network analyses of a global Hemiptera-phytoplasma-plant biological interactions database

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Abstract

A recently published global Hemiptera-phytoplasma-plant database was analyzed using graph theory and network statistics, providing a preliminary meta-analysis of host-phytoplasma associations worldwide. Preliminary results showed that Hemiptera-phytoplasma (HP) and plant-phytoplasma networks have low density and HP associations also show a modular and nested structure, suggesting that different phytoplasmas occupy exclusive ecological compartments of association with their hosts.

Keywords: ecological network, graph theory, leafhopper, planthopper, psyllid, plant pathogen

Introduction

Phytoplasmas belong to a lineage of bacteria (phylum *Tenericutes*, class *Mollicutes*) responsible for major economic loss in cultivated crops and other plants (Strauss, 2009). The great phyletic diversity, widespread present-day geographic distribution, and association of the group with a wide variety of host species, suggest that the group has been evolving in close association with its plant hosts and hemipteran vectors for millions of years (Trivellone *et al.*, 2019). It has long been recognized that microbial associates, including pathogens, play crucial roles in mediating trophic interactions between plants and insects (Janson *et al.*, 2008), and that both indirect and direct interactions may drive ecological and evolutionary processes contributing to dispersal, local adaptation and speciation (Biere and Tack, 2013). However, despite the extensive research devoted to understand the mechanisms that lead to infection and spread of phytoplasmas, no prior attempts have been made to examine patterns of association among phytoplasmas, their plant hosts and the hemipteran insect vectors at a global level. An online database of global Hemiptera-Phytoplasma-Plant (HPP) interactions has been recently published to summarize the information available in the literature (Trivellone, 2019). The preliminary analyses suggested that several phytoplasma strains are widespread and infect a wide variety of hosts, but many groups appear to be more restricted, with a tendency to be associated with particular biogeographic regions and/or plants and hemipteran families or subfamilies. In this study the general patterns of infection by phytoplasmas on insect (Hemiptera) and plant hosts are analyzed, and preliminary results of network analyses of host-phytoplasma interaction data are presented.

Materials and Methods

Datasets

Analyses were carried out on two datasets extracted from the HPP database (Trivellone, 2019): Hemipteran-Phytoplasma (HP) and Plant-Phytoplasma (PP). The entire HP dataset consists of co-occurrence data for 262 species worldwide, with 246 insect hosts (H, all belonging to the suborder Auchenorrhyncha and family Psyllidae) and 16 phytoplasma groups (P). The list of insect hosts includes species with status of either competent (211) or potential (35) phytoplasma vector as defined by Trivellone (2019). The entire PP dataset is composed of 672 species, with 639 plant hosts (Pl) and 33 phytoplasma groups (P). The list of plant hosts includes species resulted positive for the phytoplasma presence.

Network Statistics

Network representation of biological relationships usually considers organisms as nodes and their direct or indirect interactions as links (ball-and-stick diagram), summarizing the overall trend of a collection of independent studies in a single graph. To reveal patterns of biological associations, the network topology was examined using properties such as density and degree of network centrality. The HP and PP

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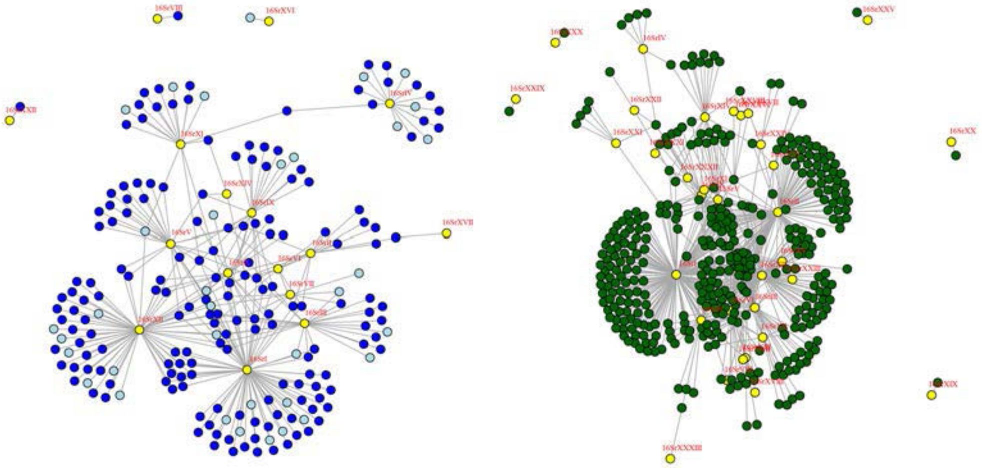

Figure 1. Network representation of the interactions between, phytoplasma groups and their potential (light blue) and competent (dark blue) hemipteran vectors (left graph) and phytoplasma groups (yellow nodes) and plant hosts (green) (right graph).

datasets were analyzed and graphed using *igraph* package (Csardi and Nepusz, 2006) in R (R Core Team, 2014). Measures of modular structure and nestedness in the HP network were also calculated. Modularity describes the degree to which a network can be grouped in modules (*i.e.* groups of nodes more densely connected to each other than with other nodes). The standard BRIM algorithm (Barber, 2007), which utilizes the Q index, was used. Q represents how often a particular ordering of phytoplasmas and hosts into modules corresponds to interactions that are primarily inside a module ($Q \approx 1$), primarily outside ($Q \approx -1$) or somewhere in between ($-1 < Q < 1$). Nestedness occurs when specialists from both sets of species interact preferentially with generalists. The NODF algorithm (Almeida-Neto *et al.*, 2008) was applied, and the network was considered nested if the observed NODF value was higher than that predicted by a null model. A Bernoulli random null model was used to measure the statistical significance of modularity and nestedness.

Results

In Figure 1, phytoplasma groups (yellow), competent (dark blue) and potential (light blue) vector species are shown as nodes. The proportion of links from all possible in the network is 0.012. The 16SrI and XII phytoplasma groups are associated with the largest number of insects with 77 and 65 competent and potential vectors, respectively.

The proportion of links from all possible in the PP network (Figure 1) is 0.008. The 16SrI, -II and -XII phytoplasma groups are associated with the largest number of plants with 201, 106 and 116 species, respectively. The entire HP dataset showed significant modularity (Q = 0.57, *z*-score = 5.11, number of modules = 14) and nested structure (NODF = 0.18, *z*-score = 45.62). However, 12 out of 14 modules are composed of only one phytoplasma group, it was not possible to calculate modularity and nestedness within internal modules.

Discussion

Understanding the structural organization of biological networks using topological measures gives clues to the evolutionary processes that may produce the observed host-phytoplasma associations. These preliminary results showed that HP and PP networks have low density, and HP associations also show a modular and nested structure, suggesting that different phytoplasmas occupy exclusive ecological compartments of association with their hosts. Statistical analyses to detected modularity and nestedness of PP dataset are still ongoing.

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