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Original Research Article

# Effectiveness of dynamic quarantines against pathogen spread in models of the horticultural trade network

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ABSTRACT

The live plant nursery trade is a potential vector for pests and pathogens, which can spread to natural and developed environments with unintended ecosystem consequences. Simulated, approximately scale-free, tiered horticultural trade networks consisting of growers, wholesalers, and retailers were used to study the efficacy of quarantine inspection and isolation procedures for reducing the spread of infected materials to consumers. The quarantine algorithm temporarily isolated infected nurseries from the rest of the trade network, rewiring the affected trade connections to unquarantined nodes, until the infection was reduced below the detection threshold, at which time the formerly infected nursery was reincorporated into the trade network.

Nodes were inspected for infection at regular intervals. Increasing the inspection interval resulted in higher levels of infection with large, system-wide oscillations whose period that matched the inspection interval. The timing of quarantine inspections of the largest hub in the grower tier drove the dynamics of the entire network. Increasing the proportion of growers or wholesalers increased infection level in most networks. Increasing the connectivity within the grower and wholesaler tiers led to large increases in mean infection levels. Focusing quarantine inspection efforts on hubs in the grower and wholesaler tiers may be the most efficient method for reducing the level of infected plant material sold by retailers in real plant trade networks.



## 1. Introduction

The international market for live horticultural plants is the leading pathway for the spread of exotic plant pathogens into novel environments (Liebhold et al., 2012). Once invasive pathogens enter an area, they can spread to new locations through domestic nursery trade networks, and ultimately into natural environments such as forests where they have the potential to alter local ecological processes. At present, inspections and quarantine of plant materials are the primary strategies used to restrict invasive pathogen spread through international and domestic horticultural trade networks (Liebhold et al., 2012; Schrader and Unger, 2003). Detection efforts during scheduled inspections attempt to locate the presence of invasive pathogens in locations where horticultural plants are grown or sold, from which positive cases lead to quarantine measures intended to prevent the further spread of infected products to consumers or other businesses in the trade network. Within the US, contemporary approaches for determining the timing of inspections and quarantine measures include fixed intervals, for example annual inspections of plant producers (MD Dept. of Agriculture, 2015). In many states inspections are required for all inter- and intra-state shipments of nursery materials (WA Dept. of Agriculture, 2015), while some states invest additional resources on county-level inspections (CA Dept. of Food and Agriculture, 2015).

Two examples (out of many) high-profile cases of the human-mediated spread of plant pathogens via the commercial plant trade highlight the need for theoretical and empirical research that aims to characterize both the structure and behavior of horticultural trade networks and the effectiveness of control strategies. White pine blister rust was carried to the east coast of the US on *Pinus strobus* (eastern white pine) seedlings from European nurseries around 1898 (Spaulding, 1911; Spaulding and others, 1929). It was subsequently transported to British Columbia via the plant trade and has since become a serious pathogen of all species of North American white pines impacting timber harvests and forest species composition (Kinloch, 2003; Mielke, 1943). Control methods for white pine blister rust infection include some of the earliest plant quarantines in the US, which restricted foreign importation and domestic movement of white pines and species in the genus *Ribes*

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(the alternative host for white pine blister rust; Liebhold et al., 2012; Weber and others, 1930). The horticultural trade has also been implicated in the spread of the recently described oomycete *Phytophthora ramorum*, the invasive plant pathogen responsible for sudden oak death in the western USA and sudden larch death in the UK (Goss et al., 2010, 2009). *P. ramorum* has been isolated from nurseries in Canada, Great Britain, many US states, and several continental European countries (Elliott et al., 2009; Frankel, 2008; Goss et al., 2010; Werres and Kaminski, 2005). Escape from infected nurseries and the sale of infected plant material are implicated in sudden oak death infestations in several forested sites in California (Mascheretti et al., 2009, 2008). Natural dispersal in *P. ramorum* is primarily short distance (<4 km; Hansen et al., 2008) so long-distance human-mediated dispersal pathways, such as the transportation of infested soil on hikers' shoes and transmission via the plant trade network are key pathways for regional and continental dispersal (Davidson et al., 2005; Hansen et al., 2008).

Network theory provides a framework to examine the spread of plant pathogens via the horticultural trade. Theoretical research into the structure and behavior of plant trade networks has provided key insights to help predict and control future outbreaks (Jeger et al., 2007; Pautasso and Jeger, 2014). Networks can be modeled as mathematical graphs consisting of a set of entities, referred to as nodes or vertices, whose relationships with other entities are represented by connections, referred to as edges or links (Newman, 2003). Relationships can be mutual in undirected networks, or one way in directed networks. The in and out degree of a node are the number of edges terminating at or originating from the node, respectively. In a network model, the edges can represent any kind of relationship among nodes, for example trading relationships among businesses or social contacts among people (Newman, 2003). The pattern of edges, i.e. the topology or contact structure, determine properties of networks such as how efficiently information, or infection, can be transmitted among nodes (Shirley and Rushton, 2005). A number of studies have examined the spread of infected plant material through hypothetical trade networks (Moslonka-Lefebvre et al., 2009; Pautasso et al., 2010b; Pautasso and Jeger, 2008). These models have provided insights into disease spread through the plant trade network such as the importance of the degree of the starting node for the final size of an epidemic, and the need to focus efforts on the wholesalers in horticultural trade networks who have balanced in- and out-degrees (Pautasso et al., 2010a,b).

Epidemic models incorporating quarantine algorithms have produced a range of results pertinent to modeling the horticultural plant trade network. Arino et al. (2007) found a reduction in mean number of infected individuals resulting from a quarantine that restricted migration of individuals. Meanwhile, Sattenspiel and Herring's (2003) study on the 1918/1919 flu epidemic in Canada revealed minimal difference between quarantine and non quarantine treatments when mobility was already low. Hethcote et al. (2002) found that implementing quarantine could induce oscillations in the endemic infection level. These varied results may in part reflect the variety of ways quarantine can be implemented and the diverse characteristics of the structure of quarantine models. An example of the importance of model design is found in the Arino et al. (2007) model, which includes spatial dynamics. In that model two levels of quarantine efficacy, internal and external, were simulated. In the context of a network quarantine model, these two levels could correspond to quarantine within and between nodes. In this example, the nodes represent cities or trading partners with the internal and external quarantine corresponding to efforts to minimize local spread and long-distance jumps, respectively. Likewise, models of the introduction of invasive plants via the horticulture industry have produced insights into how regulatory measures, such as fees or taxes, interact with ecological and market factors to influence the socially optimal size of the horticultural network (Barbier et al., 2011; Barbier and Knowler, 2006).

While existing network models of pathogen spread have undoubtedly produced knowledge contributing to the control of invasive pathogens in the horticultural trade network, much of the literature on network model applications in plant science has focused on networks with fixed contact structure (Pautasso and Jeger, 2014). The contact structures of real trade networks, however, are likely to evolve over time in response to market forces and regulatory actions. Previous modeling work has shown that temporal heterogeneity in the contact structure of a network can affect the basic reproductive rate and the final number of cases in network epidemic models (Stehlé et al., 2011). In a study of the effectiveness of a dynamic quarantine algorithm on social contact networks, Lagorio et al. (2011) demonstrated that the size of an epidemic can be reduced by increasing the likelihood that infected individuals are isolated from uninfected individuals within the network. In this study, the epidemic was able to spread throughout the networks until the quarantine intensity reached a critical threshold, above which the epidemic failed to spread (Lagorio et al., 2011). Modeling work is needed to determine the extent to which horticultural trade networks exhibit similar behavior, and how the details of quarantine implementation might affect the efficacy of control measures.

The objective of this research is to evaluate the effectiveness of dynamic quarantine measures by simulating pathogen spread in idealized plant trade networks with topologies that change in response to quarantine. Specifically, the model simulates how dynamic quarantine measures constrain pathogen spread throughout a tiered horticultural trade network consisting of growers, wholesalers, and retailers. Here dynamic quarantine to refer to the isolation of infected nurseries from the larger trade network by the rewiring of trade connections until the infection falls below a detection threshold. This research aims to (1) characterize the effect on epidemic spread of varying the quarantine inspection interval in different tiers of nodes in trade networks; (2) evaluate the effectiveness of focusing quarantine efforts on highly connected nodes; (3) characterize the relative efficiency of quarantines on networks with different proportions of growers, wholesalers, and retailers; (4) characterize the relative efficiency of quarantines on networks with varying levels of connectedness within and among growers, wholesalers, and retailers.

## 2. Methods

An epidemic network modeling approach was used to simulate spread of pathogens through idealized horticultural trade networks. Networks consisted of three tiers of nodes representing growers, wholesalers, and retailers. Directed trading relationships among businesses were represented by inter- and intra-tier edges. Network topology was determined stochastically for each simulation replicate. Infected plant material was spread deterministically among nodes via the edges. A stochastic quarantine measure randomly rewired edges away from infected nodes. A detailed description of the methods following the ODD protocol (Overview, Design concepts, Details; Grimm et al., 2010) is provided in the supporting materials. The following is a brief overview describing the key aspects of the model design and implementation.

### 2.1. Simulated networks: motivation and model construction

To test the effectiveness of quarantine on different sizes of networks, we simulated small (100 node) and large (1000 node) directed, hierarchical networks. The large network size was representative of the approximate number of nurseries in the