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Identifying local drivers of a vector-pathogen-disease system using Bayesian modeling

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Abstract

'Bois noir' is a phytoplasma-mediated grapevine yellows disease that causes great economic damage in European vineyards. Previous studies have examined habitat relationships on a regional scale, which help to better understand the large-scale epidemiology. Local drivers, such as micro-habitat preferences of the vector (*Hyalesthes obsoletus*, a cixiid planthopper), or local interactions with reservoir host plants, however, are still poorly understood, although this knowledge is crucial for developing site-specific management strategies.

Here, we examined the local environment-species relationships of a phytoplasma-mediated grapevine disease on a scale of 15 m in a 2.9 ha vineyard using: (i) data on elevation and habitat types; (ii) cover of host plants *Urtica dioica* and *Convolvulus arvensis* over three seasons, (iii) vector monitoring over four seasons; (iv) genetic tests for phytoplasma presence in the vector; and (v) inspection of 6056 grapevine plants for visual symptoms of the 'bois noir' disease. The data were analyzed in a joint causal model that describes the interplay between vector, pathogen, disease and environment, estimated with Bayesian inference.

Our results indicate that surrounding natural and semi-natural vegetation (fallow land, forest and managed agricultural land) and high density of the major host plant *U. dioica* are associated with an increase in vector population densities. Higher vector population densities at low availability of *U. dioica* were associated with higher phytoplasma infection rates in the vector. The prevalence of disease symptoms in grapevine plants was nonetheless more affected by grapevine cultivar and higher elevation than by the estimated availability of infected vectors.

The results of our local analysis support current bois noir management recommendations stating that (1) removal of the host plant *U. dioica* should be best carried out in either spring or autumn; and (2) grapevine cultivars are unequally susceptible. Moreover, we provide evidence that *U. dioica* control before the flight period may result in low *U. dioica* densities and high *H. obsoletus* population densities, causing an increase in vector infection rates and disease pressure.

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Zusammenfassung

Die Schwarzholzkrankheit (Bois noir) ist eine durch Phytoplasmen ausgelöste Vergilbungskrankheit auf Reben, welche erhebliche ökonomische Schäden im europäischen Rebbau verursacht. Bisherige epidemiolgische Studien zu den Habitatassoziationen von Bois noir konzentrierten sich auf die regionale Ebene. Lokale Standortfaktoren, wie das vom Überträgerinsekt (*Hyalesthes obsoletus*, Hemiptera: Cixiidae), bevorzugte Mikroklima oder lokale Interaktionen mit den Wirtspflanzen, wurden bis jetzt kaum untersucht worden. Jedoch sind gerade diese notwendig für die Entwicklung standortspezifischer Bekämpfungsstrategien.

Wir untersuchten die kleinräumigen "Umwelt-Art-Beziehungen" dieser Vergilbungskrankheit in einer räumlichen Auflösung von 15 m in einem 2.9 ha großen Rebberg. Dabei verwendeten wir die folgenden Daten: (i) Höhe (m ü. NN) und Landschaftskontext; (ii) Deckungsgrad von den Wirtspflanzen *Urtica dioica* und *Convolvulus arvensis* aus drei Jahren; (iii) Gelbfallenfänge von *H. obsoletus* aus vier Jahren; (iv) molekulare Phytoplasmennachweise in Überträgerinsekten; und (v) Symptomausprägung der Schwarzholzkrankheit auf 6056 bonitierten Rebstöcken.

Unsere Ergebnisse zeigten, dass natürliche und naturnahe Bereiche (wie Brachflächen, Wälder, Grasflächen) in der näheren Umgebung und hohe Deckungsgrade der wichtigsten Wirtspflanze, *U. dioica*, mit zunehmenden Fangzahlen des Überträgerinsektes korrelierten. Höhere Populationsdichten korrelierten außerdem mit höheren Durchseuchungsraten bei geringem Vorkommen der Wirtspflanze *U. dioica*. Das Auftreten von Krankheitssymptomen an Weinreben war allerdings deutlich stärker beeinflußt von der Weinsorte und der Meereshöhe als vom geschätzten Vorkommen an infizierten Überträgerinsekten.

Die Modellergebnisse unserer kleinräumigen Untersuchung bestätigen bestehende Managementstrategien, dass (1) die Wirtspflanze *U. dioica* im Frühjahr oder Herbst bekämpft werden sollte und dass (2) die Ausprägung der Symptome in Abhängigkeit von der jeweiligen Rebsorte unterschiedlich stark sind. Darüber hinaus zeigen wir, dass eine Bekämpfung von *U. dioica*, welche eine nicht vollständige Entfernung der Wirtspflanze zu Folge hat, bei anschließender hohen Populationsdichte des Vektors, eine hohe Durchseuchung des Vektors und damit höheren Befallsdruck auf die Weinreben zur Folge haben kann.

Keywords: Auchenorrhyncha; Bayesian inference; Bois noir; Disease; Epidemiology; Grapevine; *Hyalesthes obsoletus*; Phytoplasma; Local-scale; *Vitis vinifera*

Introduction

Phytoplasma bacteria cause a range of diseases in economically important crops, such as fruit trees and grapevines. The bacteria form complex biological disease systems, typically together with one or more insect vectors and one or more host plants. Phytoplasma are vectored by phloem-sucking insects that belong to the planthopper, leafhopper and psyllid families (Auchenorrhyncha and Stenorrhyncha, Hemiptera) (Weintraub & Beanland 2006). Unless a long evolutionary adaptation between pathogen and host plant has taken place (Elliot, Adler, & Sabelis 2003; Maixner 2010), infected plants have reduced fitness and develop characteristic symptoms such as phyllody (parts of the flower turn into leaves), witches' broom, chlorotic leaves and shriveled fruits (Hogenhout et al. 2008). Because of the complex interplay between vector ecology (habitat requirements, formation of host races (Imo, Maixner, & Johannesen 2013)), phytoplasma ecology (virulence, evolution) and the infected plants (latency, susceptibility), phytoplasma epidemiological systems are typically relatively difficult to predict.

Here, we investigated the ecological causes of 'bois noir' (BN), a phytoplasma grapevine disease that is widespread in European vineyards. The causal agent, '*Candidatus* Phytoplasma solani' (Quaglino et al. 2013), belongs to the stolbur (16SrXII-A) group (Daire, Boudon-Padieu, Berville, Schneider, & Caudwell 1992; Maixner, Ahrens, & Seemüller 1994). Many plants are known to naturally harbor '*Ca.* Phytoplasma solani' (Sforza, Bourgoin, Wilson, & Boudon-Padieu 1999; Sharon et al. 2005). The predominant host plants depend on the geographical region. In Germany, both field bindweed (*Convolvulus arvensis* L., Convolvulaceae) and stinging nettle (*Urtica dioica* L., Urticaceae) are considered to be the major host species (Maixner & Langer 2006). Two distinct phytoplasma strains, tuf type I and II, have been shown to be associated with *U. dioica* and *C. arvensis*, respectively (Langer & Maixner 2004).

Field-monitoring studies and transmission trials have identified *Hyalesthes obsoletus* Signoret (Auchenorrhyncha: Cixiidae) as the main BN vector in SW Germany (Breuer, Fahrentrapp, & Michl 2008; Maixner 1994). The insect vector acquires the phytoplasma when feeding on the roots of its host-plants during larval development in the soil (Kaul, Seitz, Maixner, & Johannesen 2009). Despite being polyphagous, the insect vector can only complete its life cycle on its host plants, which function as a permanent source of phytoplasma