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Modelling local and long-distance dispersal of invasive chestnut gall wasp in Europe

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ABSTRACT

The chestnut gall wasp, *Dryocosmus kuriphilus*, was found in Europe in 2002 in the Piedmont region (Italy), later it spread progressively to the rest of Italy and its presence is nowadays confirmed in other European countries. The discontinuous pattern of spread in Italy, and the pattern of increase of the total invaded area over time are consistent with a stratified dispersal mechanism. The spatio-temporal dynamics in Europe have been investigated by a stratified dispersal model. The model considers local population growth, spatially continuous short distance random dispersal (SDD) and discrete events of long distance dispersal (LDD), and it has been applied to summarize the available information on the species biology and distribution in Europe. The model allowed the interpretation and the reconstruction of a realistic dynamics of the chestnut gall wasp colonization of Europe in the period 2002–2009, confirming the hypothesized mechanism of stratified dispersal and deriving parameter estimates for the functions describing SDD and LDD. The values of the speed of the population front of invasion are normally distributed with mean 6.6 km/year, significantly less than the values reported in literature. The estimated travelled distances per LDD events are gamma-distributed with mean 76 km. The number of LDD events per time unit appeared to be the critical parameter influencing the rate of colonization of the chestnut forest areas. The estimated model can be used to provide projections (scenarios) on the likely course of future events of Europe colonization based on appropriate assumptions on the biology of the invasive species and the efficacy of management measures in controlling population growth and dispersal via the LDD.

1. Introduction

The "oriental chestnut gall wasp" *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera; Cynipidae) is a univoltine thelytokous (females only) species (Moriya et al., 2003). The cynipid wasp is native to China where it disrupts the growth of chestnut trees (*Castanea* spp.) by inducing gall formation on new shoots and leaves (Ôtake, 1980). Adult females are about 2 mm in length and emerge from the gall during May and July to disperse and lay eggs in chestnut buds that will develop the following spring. Egg hatches in a month and first larval stage remains within the egg and overwinters in plant buds. At bud burst the following spring, larval feeding induces the formation of green or rose-coloured galls (of 5–20 mm in diameter), in which the cynipid develops to adult emergence. Because of its capacity to interact and limit the chestnut trees growth, *D. kuriphilus* is considered one of the most dangerous pests of the genus *Castanea*. It has been designated as a quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO, 2005) and regulated by the European Commission with specific emergency measures in order to prevent its introduction and spread among the European Member States (Commission Decision 2006/464/EC of 27 June 2006). *D. kuriphilus* was accidentally introduced from China to Japan, where its presence was first recorded in 1941 (Yasumatsu, 1951), to Korea in 1958 (Cho and Lee, 1963), and to the United States in 1974 (Payne et al., 1975) and Nepal in 1999 (Abe et al., 2007). Its recent and rapid invasion of Europe raises important issues concerning its dispersal mechanisms and its potential diffusive capacity at the population level. Answering these questions has important implications not only for understanding *D. kuriphilus* biology and ecology, but also for its management, especially in the areas of recent invasion.

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Different processes are involved in the spread of the chestnut gall wasp. Natural process of dispersal of the adults is due to active flight and wind-assisted passive transportation. The latter mechanism is likely to constitute the main natural dispersal mechanism as adults are not strong fliers, and rely on wind for dispersal (Oho and Shimura, 1970). This dispersal depends on the speed and the direction of the prevailing wind, with low wind speed stimulating flight initiation, wind speed higher than 0.73 m/s inhibiting the flight, and wind speed above 2.15 m/s enhancing passive transport (Oho and Shimura, 1970). Adults blown by the wind have a high risk of mortality and failure to reproduce because they are unlikely to land on suitable host plants significantly reducing the efficacy of this modality of dispersal. Human-assisted dispersal occurs via transport of adults (e.g., in clothes or vehicles) or on infested plants and scions and budwood (Oho and Shimura, 1970; Rieske, 2007; Graziosi and Santi, 2008). The latter is probably the main mechanism for the dispersal of immature stages and represents the major pathway for colonization of new more distant areas. Given the present distribution of *D. kuriphilus* and the number of countries that have been invaded, human assisted spread can be considered a major mechanism (Rieske, 2007; Graziosi and Santi, 2008).

Various interpretation and estimates of the rate of *D. kuriphilus* spread at population level have been proposed. According to Payne (1981), the adults of *D. kuriphilus* can spread by natural means (active and wind-assisted flight) at a rate of approximately 24.1 km/year. Rieske (2007) presents a map illustrating the dispersal pattern of the gall wasp in North America from 1974 to 2006 and estimates a spread rate of 25 km/year. Graziosi and Santi (2008) analyzed the spread of the pest in 12 Italian regions during 2002–2008, and estimated the rate of natural expansion in Italy as 25 km/year. Despite the convergence in the estimates, aspects of the dispersal mechanisms and rates remain to be clarified: (i) The estimate of the spread rate was interpreted by Rieske (2007) as an average distance dispersed per year obtained by dividing the distance of the invasion front from the supposed site of introduction by the number of years since first detection. This estimate provides an average rate of spread, neglecting any interpretation of the underlying dispersal mechanisms and their relative contribution to the pattern of spread. (ii) Interpreting the spread as continuous random dispersal is questionable. For example, a simple visual analysis of maps representing the spread of *D. kuriphilus* in the Piedmont region (Italy) during the first years of the invasion shows that the rate of 25 km/year reported by Graziosi and Santi (2008) is excessive. In the meantime the proposed rate does not accurately account for the fast colonization observed in Italy during 2002–2009. The spread in Italy was not continuous in space and, in many cases the invasion produced new colonies clearly separated from the area already invaded. This pattern is consistent with a stratified dispersal mechanism (Liebhold and Tobin, 2008; Nathan et al., 2008) with a component of long distance dispersal in which human transportation of both adults and immature stages playing a key role.

To obtain a precise interpretation of the pattern and rate of expansion range, we developed a modelling approach describing the spread of *D. kuriphilus* in Europe from 2002 to 2009 based on stratified dispersal derived from a model recently proposed as a management tool for *D. kuriphilus* ((EFSA Panel on Plant Health, 2010). Our study further develops the model structure and refines parameter estimates. Furthermore, the reference database for model development and calibration has been extended and updated by including data obtained from national and regional phytosanitary services. The dispersal model describes the spread dynamics at the population level (macroscopic level) based on assumptions about dispersal mechanisms at the individual level (microscopic level). In most of the cases, information was not available on the dispersal processes causing variation in the spatial patterns of observed gall wasp populations (e.g., the origin of propagules infesting new areas and the modality of colonization dispersal). Consequently, only interpretation at the macroscopic level of the spatial dynamics of the occupied area is considered in the model. The analysis is based on the hypothesis that *D. kuriphilus* follows two different types of dispersal: local or short distance dispersal (SDD) and long distance dispersal (LDD). The combined process of SDD and LDD is called stratified dispersal (Shigesada et al., 1995; Nathan et al., 2003; Liebhold and Tobin, 2008).

At the population level, SDD results in the continuous spread of the colonized area through the progressive spread of the invasion front. At the individual level, the mechanism might be interpreted as the results of the natural random movement of the adults with dispersal due to natural (e.g., wind) or artificial driving forces (direct human transportation).

At the population level, LDD is the result of discrete events that lead to the establishment of new infestation centres separated from the closest infested area by a non-infested zone. At the individual level, LDD processes might be interpreted as the consequence of artificial dispersal events due mainly to the transportation of biological material to new areas. Each new infestation centre is at the origin of a new SDD process, resulting in an infested area that expands over time.

The proposed model attempts to summarize the available information on the *D. kuriphilus* biology and the data on its distribution in Europe relevant to the analysis of the mechanism and rates of dispersal. The objective is to analyze the spread of chestnut gall wasp that allows the reconstruction of the dynamic of European colonization during the period 2002–2009. Model parameter for the functions describing SDD and LDD were derived from these data.

2. Methods

2.1. Data

2.1.1. Distribution of Castanea spp. in Europe

A distribution map for chestnut, including both natural and naturalized occurrence, was produced by members of the European Forest Genetic Resources Programme (EUFORGEN) Noble Hardwoods Network. The maps are based on maps published by Maurer and Fernández-López (2001) and Bounous (2002). The dataset can be downloaded in shapefile format from the website at www.euforgen.org. A higher detailed distribution map for *Castanea*, highlighting the main area of chestnut cultivation is reported in Conedera et al. (2004), that unlike the EUFORGEN dataset, does not include potential areas of *Castanea* occurrence. Conedera et al. (2004) present the updated and digitalized form of the original maps provided by the Chestnut Working Group in the 1950s (Première session du groupe des experts du chataignier – Italie, Suisse, 8–19 Oct 1951) for many European countries (e.g., France, Greece, Italy, Portugal and Spain).

The distribution of chestnut used in our work includes areas in Conedera et al. (2004) falling inside the EUFORGEN distribution buffered by a 5 km surrounding zone. Chestnut areas detailed in the Conedera et al. (2004) distribution falling outside the EUFORGEN distribution were buffered with a 1 km surrounding zone. The resulting areas were intersected with the EUFORGEN distribution to include the latest estimates. The resulting distribution map for chestnut is depicted in Fig. 1, and it may exclude some existing *Castanea* areas and/or include areas where *Castanea* is not currently present. These uncertainties could affect the distribution of *D. kuriphilus* outlined in the next section. Vector format distribution maps were converted to a raster format using a 1 km^2 cell size and gridded in ASCII format used as input to the model. As distance is an important variable, the projection selected to represent