




Climatic and anthropogenic factors affect *Ailanthus altissima* invasion in a Mediterranean region

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Abstract *Ailanthus altissima* is an aggressive invasive tree worldwide, but the ecological factors that lead to the spread of this species in Mediterranean ecosystems are still unclear. Here we aim to identify such factors, focusing on the interaction of human activity with climatic conditions. We determined the occurrence and abundance of *Ailanthus* in 240 sites and studied their relationship with 20 variables representing climatic, geographic, and topographic factors, as well as land use, in the region of Campania (southern Italy). Overall, we found that temperature and rainfall in Campania are suitable for *Ailanthus*, with the only major constraint being the temperature at an altitude exceeding 900 m a.s.l.. We found that

Ailanthus is unable to spread where the mean annual temperature is lower than 11.1 °C. By contrast, precipitation variables showed poor correlation with *Ailanthus* distribution, suggesting that rainfall in the selected study sites is suitable to sustain the growth of this tree. About land use variables, roads were the primary landscape feature along which this species spread and invaded new areas. Roads probably combine high propagule pressure and favorable growing conditions in terms of available resources i.e., light, water, and mineral nutrients, that allow *Ailanthus* to establish and spread along roadside edges in different ecosystems. In conclusion, we found that climate and human-associated variables are correlated with the current occurrence of *Ailanthus*, with the temperature being more influential at high elevation sites and road distance playing a prominent role in low elevation areas.

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Introduction

Plants can be called alien if their presence in a given area is due exclusively to human activities (Pyšek et al. 2004). The intentional or accidental human-mediated introduction of species to areas outside their native

range allows them to overcome natural dispersal mechanisms and biogeographic barriers (Blackburn et al. 2014). Biological invasions are now widely recognized as a major component of global change that can alter ecosystem diversity and functioning (Pyšek and Richardson 2010; Tarantino et al. 2019) and can promote alternative successional trajectories that may negatively affect the landscape (Gaertner et al. 2014; McKinney and Lockwood 1999; Stinca et al. 2015). The impacts of alien species may manifest: (i) by decreasing local plant species diversity (Gaertner et al. 2009; Powell et al. 2013; Vilà et al. 2011); (ii) by reducing the distinctiveness of local biological communities (Lazzaro et al. 2018; Olden and Rooney 2006); (iii) by the alteration of soil nutrient cycling processes (Bonanomi et al. 2018; Ehrenfeld 2003; Liao et al. 2008); iv) by hybridization processes of native and alien species (Ellstrand and Schierenbeck 2000; Vilà et al. 2000). Alien species have thus emerged as a defining feature of the Anthropocene (Lewis and Maslin 2015). According to Pyšek and Richardson (2010), economic costs to society of harmful invasive species involve those associated with losses of biodiversity and impaired ecosystem services, as well as the costs of controlling invasive species and reducing and mitigating their impact.

In many parts of the world, alien woody species are among the most conspicuous, damaging, and, in some cases, best-studied invasive species, shedding light on crucial aspects of invasion ecology (Richardson and Rejmánek 2011). *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), hereafter referred to as *Ailanthus*, is a deciduous dioecious tree native to eastern China and northern Vietnam that has developed into a globally invasive species, expanding on all continents except Antarctica (Kowarik and Säumel 2007). It was first introduced into Europe in the 1740s as an ornamental plant from the collection of a Jesuit priest who had mistaken it for a lacquer tree (*Toxicodendron vernicifluum* (Stokes) F.A. Barkley) and later in the nineteenth century to breed the saturniid moth *Samia cynthia* (Drury 1773) to produce silk fabric (Conedera et al. 2014; Fotiadis et al. 2011).

Ailanthus is now considered an invasive species because of its rapid spread due to its high seed production and its ability to reproduce from stump sprouts and suckers (Casella and Vurro 2013; Vilà et al. 2006). Yet it is believed to invade natural

vegetation only if some form of disturbance has provided safe sites for its establishment (Kowarik 1995). *Ailanthus* produces from several hundred thousand to several million seeds in a single year, with large inter-annual variation and tree size-dependent effects (Bory and Clair-Maczulajtys 1980; Martin and Canham 2010; Wickert et al. 2017). This species uses wind as primary and water as secondary dispersal vectors (Kowarik and Säumel 2008). In addition, the species is capable of vigorous clonal reproduction and resprouting when cut (Kowarik 1995), thereby increasing its invasive potential. Indeed, it can create dense thickets which outcompete native trees (Rebbeck and Jolliff 2018). In Italy, *Ailanthus* is now firmly established in all regions and is the most common alien species, together with *Robinia pseudoacacia* L., along railway lines (Celesti-Grappo and Accogli 2010). In this regard, railways and roads have been widely shown to facilitate the spread of invasive plants (Kowarik and Von der Lippe 2011; McAvoy et al. 2012; Milton and Dean 1998; Mortensen et al. 2009).

In recent decades several studies have focused on the main climatic, geographical, and anthropogenic correlates which influence the spread of alien plants in many regions of the world (Arteaga et al. 2009; McAvoy et al. 2012; Rebbeck et al. 2017; Speziale and Ezcurra 2011). In this context, species distribution models combined with monitoring studies have found that *Ailanthus* distribution is limited in tropical zones as well as at high latitudes and altitudinal sites characterized by cold climates (Walker et al. 2017), indicating the important role of climatic variables in determining the potential range of this invasive species. Although *Ailanthus* conspicuously and prolifically colonizes a broad array of habitats (Kowarik and Säumel 2007), little information is available in the Mediterranean basin on the interactive effects of anthropogenic, ecological, and geographical factors on the ability of this species to become invasive. In this context, the present work aimed to explore the factors affecting *Ailanthus* distribution, focusing on the role of roads, land use and climatic factors. In this regard, we assessed the occurrence and abundance of the species in 240 sites and studied the relationship with climatic, geographic, topographic, and land use variables in Campania (Southern Italy). We tested the hypotheses that:

- (i) at low elevation, *Ailanthus* occurrence is positively associated with human disturbance, being more common in areas close to roads;
- (ii) *Ailanthus* altitudinal distribution is limited by low temperature.

Materials and methods

Study area description

Campania is situated in the southwestern part of the Italian peninsula, bounded by the Tyrrhenian Sea to the west (Fig. 1). The region exhibits highly variable environmental conditions resulting from its topography, with elevations ranging from 0 to 1923 m a.s.l. and includes the Phlegraean Islands (Ischia, Procida, Vivara, Nisida) and Capri. According to Di Gennaro (2002), 30% of Campania is made up of mountains, 40% hills, 25% plains, and 5% volcanoes. Four regions border Campania: Lazio to the northwest, Molise to the north, Puglia to the northeast, and Basilicata to the east. With its 5,820,000 inhabitants occupying 13,670 km², Campania is the most densely populated region in Italy (430 inhabitants per km²).

Assessment of *Ailanthus* distribution, and abundance

The present study was conducted from May 2018 to October 2019. Overall, 120 study areas across Campania were monitored. The areas were located on the public, two-lane country, and municipal roads, with highways excluded from the analysis. Sites were distributed in a stratified design to include elevation from 0 to 1500 m a.s.l. and the five provinces of Campania. At a local scale, the roads and geographical locations were randomly selected from Google Earth Pro™ (Google Inc., Mountain View, CA, USA) images dating 2004–2011. Thereafter, for each selected area, two paired sites were selected: one close to the road and the second randomly positioned at a maximum distance of 2500 m. Study areas had a size of 900 m² (square of 30 × 30 m). In each area ($N = 240$) we carried out field surveys to record the total cover of *Ailanthus*, as well as the diameter and height of the larger specimens. Specifically, *Ailanthus* abundance was defined as: Absent = no plants of

Ailanthus within the plot; Low = cover of *Ailanthus* plants between 1 and 30% of the total plant cover within the plot; Intermediate = between 31 and 60%; High = between 61 and 100%.

Variables associated with *Ailanthus* distribution

We selected 20 variables to evaluate their capability to explain the current *Ailanthus* distribution, which was grouped into two classes: geographical and topographical, and climatic (Table 1).

Geographical, topographical and land use variables

Geographical variables for each area ($N = 240$) included altitude and distance from the sea (Table 1). The altitude of each sampling point was assessed by digital elevation model of Campania region with 20 m steps (Altitude) using ArcGis 10.3. Instead, distance from the sea was calculated as the distance from shoreline in respect to the sampling point using the Arcview 3.2 (ESRI/Inc) extension: Nearest Features, with Distances and Bearings. The extension can calculate the distance and bearing between the centroids of the closest features as well as the distance and bearing between the closest edges of those features (http://www.jennessent.com/arcview/nearest_features.htm). Some topographic variables were used to assess the relations of *Ailanthus* to anthropic activities and were the distance from the road and distance from urban settlements. Distance from the road was calculated for each site as the distances from the nearest two-lane road. Distance from urban was obtained as the distance from the nearest human settlement and was determined using the extension “Near east Features 3.8b” (http://www.jennessent.com/arcview/nearest_features.htm) in the Arcview 3.2 environment. The minimum distances of each of the study centroids from the closest urbanized areas were determined.

Concerning the land use, the 240 points were overlaid on land cover maps (<https://land.copernicus.eu/pan-european/corine-land-cover>) to obtain information about land uses in the proximity of areas with or without the presence of *Ailanthus*. Land use classes were: (i) agriculture, defined as lands destined to agricultural activities and characterized by perturbation of soil; (ii) mixed bushes or shrubland, defined as areas where vegetations are subject to

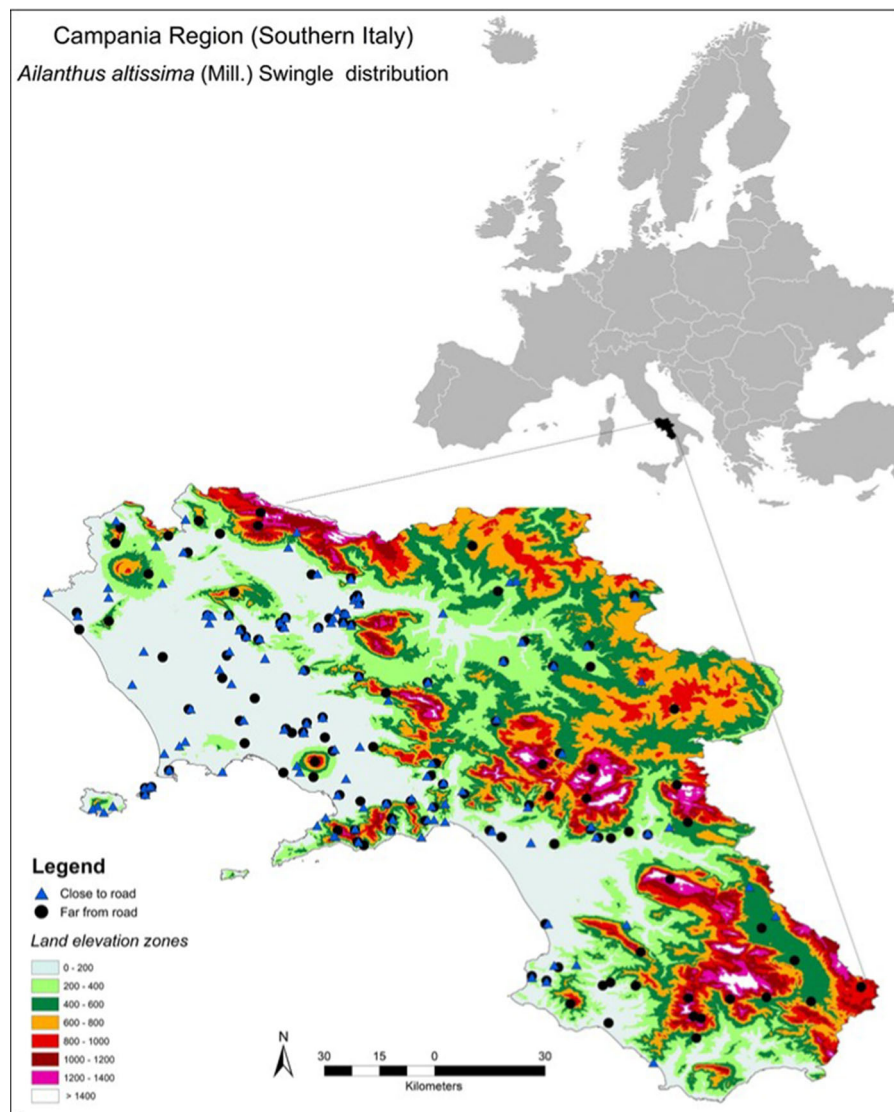


Fig. 1 Maps of Campania region showing Sampling points on the survey in the present study of *Ailanthus altissima*. Blue triangle represent sampling point in proximity of the roads and black circle represent sampling point far from road

successional process with substantial shrub encroachment; (iii) pasture, defined as lands that are permanently used (at least 5 years) for fodder production; (iv) urban, areas mainly occupied by buildings, including approach road network; (v) woodland, areas occupied by forests and woodlands with a vegetation pattern composed of native or exotic coniferous and/or broad-leaved trees; (vi) and uncultivated, the areas previously occupied by agricultural activities but recently abandoned and still dominated by herbaceous vegetation.

Climatic variables

Climatic variables representing the parameters traditionally used as species distribution predictors, namely annual and monthly temperature, seasonal thermal amplitude, and rainfall, were considered (Austin and Van Niel 2011; Walker et al. 2017) (Table 1). Climatic data were collected from the global climate database WorldClim v.2.0. (<http://www.worldclim.org>; Hijmans et al. 2005) at a spatial resolution of 1 km². The temperature in the WorldClim database represents the spatial average of grid squares adjusted according to

Table 1 List of geographical, topographical, and climatic variables used in the present study

Variable	Unit
<i>Geographical, topographical and land use</i>	
Altitude	m a.s.l
Distance from the sea	km
Distance from the road	km
Distance from urban	km
Land use	
<i>Climatic</i>	
Mean annual temperature	°C
Max temperature of warmest month	°C
Min temperature of coldest month	°C
Mean temperature of wettest quarter	°C
Mean temperature of driest quarter	°C
Mean temperature of warmest quarter	°C
Mean temperature of coldest quarter	°C
Annual precipitation	mm
Precipitation of wettest month	mm
Precipitation of driest month	mm
Precipitation seasonality	mm
Precipitation of wettest quarter	mm
Precipitation of driest quarter	mm
Precipitation of warmest quarter	mm
Precipitation of coldest quarter	mm

their average elevation. We then adjusted the effect of the elevation of individual grid squares by recalculating temperature at the level of each study site using a $0.006\text{ }^{\circ}\text{C m}^{-1}$ adiabatic lapse rate of temperature change with elevation. This lapse rate is considered appropriate for cold and temperate regions (Barry 1992). With this approach, we adjusted mean annual temperature (MAT), mean monthly, and mean quarterly temperatures. The spatial association between the values of the bioclimatic variables, of the 240 study areas, was carried out using the “Extract Multivalue to Points” routine included in the ArcGis 10.3 “Spatial Analyst tool” and analyzed for correlation with the observed absence/presence of *Ailanthus*.

Data analysis

Data obtained for the surveys were visualized as frequencies of occurrence (presence/absence). Frequencies were obtained by standardizing the number

of observations for presence and absence with respect to the total number of observations in the survey. Sampling points were grouped according to land uses in their proximity. Following each variable were divided in classes by using the distribution plot function in the Statistica 10 software. Specifically, road distance classes ranged from 0 to 2500 m, with class amplitude of 500 m. Altitude ranged from 0 to 1500 m with frequencies of occurrence of *Ailanthus* grouped in classes with an amplitude of 200 m. Distances from the nearest urban center ranged from 0 to > 2600 m and classes amplitude was 200 m.

To explore the natural distribution of the data concerning the variables used in the study, we performed a principal component analysis of the dataset. We also applied a multivariate approach to observe the specific contribution of each variable with respect to the abundance of *Ailanthus*. Before multivariate analysis raw data were normalized to avoid bias of dimensional difference affecting multivariate comparisons. Clustering for similarity of sampling points was made at a fixed threshold of 50 according to Euclidean distance ordination. Alongside the multivariate exploratory approach, a specific association between each variable and *Ailanthus* occurrence was tested by the generalized linear model (GLM) based on the Logit link in the 240 plots used for the study. Estimates of the effect were modeled according to the probability of presence of *A. altissima* and significance level fixed for *p*-values below 0.05. Furtherly, the same approach was used to test if the occurrence of *Ailanthus* is affected by selected variables close to the road defined as the range of distance from 0 to 200 m. Following, because of the multicollinearity effect a reduced set of climatic and, geographic and topographic variables were used including mean annual temperature, annual precipitation, distance from the sea, altitude, land use; and distance from the urban.

Data analyses, plots, and assignments of significance were carried out in Statistica 10 software. Multivariate data analysis was performed in Primer 7 software.

Results

Ailanthus distribution

With regard to land use, the highest frequencies of *Ailanthus* were recorded in mixed bushes followed urban and uncultivated areas (Fig. 2A). A lower frequency of *Ailanthus* was recorded under agricultural land use, with very low values found for woodland and pasture (Fig. 2A).

About the distance from the road, all presence of *Ailanthus* was within a distance of 500 m, with no occurrence at higher distances (Figs. 2B, S1). A gradual and regular decrease of presence was observed with elevation, with the highest occurrence at 870 m a.s.l. (Figs. 2C, S1). As regards distance from the nearest urban settlement, *Ailanthus* occurred variably within the first 1,600 m but was absent at greater distances (Figs. 2D, S1).

Distance from the roadside is also the variable that best explains the occurrence of *Ailanthus* with a positive estimate of absence with the increase of the distance from the road (Estimate of the effect 0.2144; $p = 0.000178$) (Table 2). Elevation above sea level and distance from the nearest urban center have lower predictive ability compared to roadside distance (Table 2).

Geographical, topographical and climatic variables

On including the geographical variables to explain abundance classes of *Ailanthus* in Campania, multivariate data analysis showed a clear separation of three groups at similarity values of 50% of Euclidean distance. Principal component analysis (PCA) explained a total of 74.9% of the variance within the dataset, with a higher contribution on the first principal component (60.9%), and lower in the second (14.0%). Segregation of the sampling points on the left side of score plots of the PCA (Fig. 3A) was mainly due to the increased elevation above sea level, distance from the road, and distance from urban areas. Inversely, the increased presence of *Ailanthus* is associated with an increase of precipitations during the driest months and in the driest quarter. Groups of sampling points with the increased presence of *Ailanthus* were associated with the increase of minimum temperature in the coldest months, mean temperature in the warmest

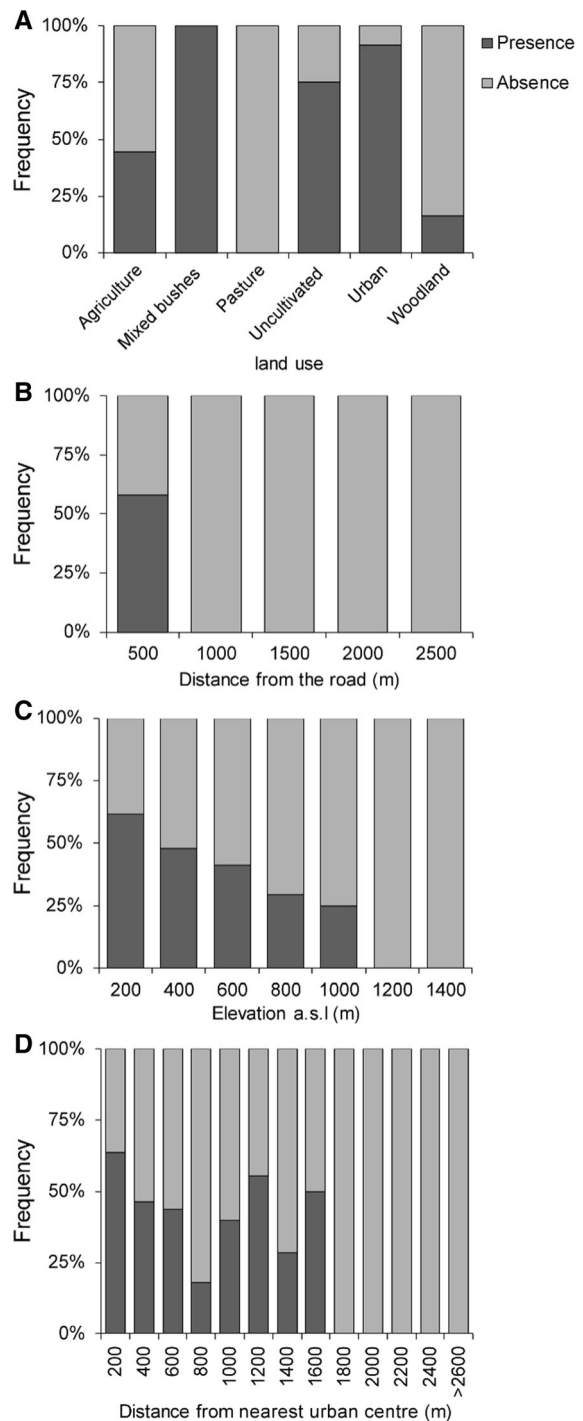


Fig. 2 Stacked bar chart showing frequencies of presence/absence of *Ailanthus altissima* in the 240 plots used for the survey. Plots are grouped according to classes of land uses (A), distance from the road (B), elevation above sea level (C), and distance from the nearest urban center (D)

Table 2 Result of Generalized linear model GLM based on Logit link function estimating significant variation in *Ailanthus altissima* occurrence in the 240 plots used for the study

Parameter estimates = occurrence
 Distribution: BINOMIAL, Link function: LOGIT
 Modeled probability that occurrence = Presence

Variables	Level of effect	Estimate	Standard error	Wald stat	Lower CL 95%	Upper CL 95%	<i>p</i> value
Intercept		220.9117	995.923	0.04920	− 1731.06	2172.886	<i>0.824457</i>
Mean annual temperature		− 1.4450	0.777	3.45879	− 0.08	2.968	<i>0.062916</i>
Max temperature warmest month		− 0.5449	0.534	1.04241	− 0.50	1.591	<i>0.307262</i>
Min temperature coldest month		− 0.5114	0.410	1.55809	− 0.29	1.314	<i>0.211945</i>
Mean temperature wettest quarter		− 0.1826	0.105	3.00744	− 0.02	0.389	<i>0.082883</i>
Mean temperature driest quarter		0.1756	0.133	1.73403	− 0.44	0.086	<i>0.187897</i>
Mean temperature warmest quarter		2.6015	1.114	5.45010	− 4.79	− 0.417	<i>0.019567</i>
Mean temperature of coldest quarter		0.2298	0.646	0.12654	− 1.50	1.036	<i>0.722049</i>
Annual precipitation		− 0.1039	0.110	0.89537	− 0.11	0.319	<i>0.344027</i>
Precipitation of wettest month		0.8134	0.463	3.08367	− 1.72	0.094	<i>0.079082</i>
Precipitation of driest month		− 0.5674	0.866	0.42894	− 1.13	2.265	<i>0.512509</i>
Precipitation seasonality		0.0154	0.842	0.00034	− 1.67	1.635	<i>0.985397</i>
Precipitation of wettest quarter		− 0.0985	0.269	0.13406	− 0.43	0.625	<i>0.714262</i>
Precipitation of driest quarter		0.2155	0.576	0.13993	− 1.34	0.914	<i>0.708354</i>
Precipitation of warmest quarter		− 0.0958	0.056	2.96049	− 0.01	0.205	<i>0.085322</i>
Precipitation of coldest quarter		0.1133	0.115	0.97141	− 0.34	0.112	<i>0.324329</i>
Elevation A.S.L		0.0112	0.019	0.34766	− 0.05	0.026	<i>0.555442</i>
Distance from the Sea (Km)		− 0.0638	0.081	0.62221	− 0.09	0.222	<i>0.430228</i>
Distance from the road (m)		− 0.2144	0.057	14.04972	0.10	0.326	<i>0.000178</i>
Distance from urban (m)		− 0.0014	0.001	1.35696	0.00	0.004	<i>0.244065</i>
Land use	Woodland	− 2.1331	984.964	0.00000	− 1928.36	1932.627	<i>0.998272</i>
Land use	Pasture	− 5.9064	3517.408	0.00000	− 6899.90	6888.086	<i>0.998660</i>
Land use	Uncultivated	− 6.0008	984.964	0.00004	− 1924.49	1936.495	<i>0.995139</i>
Land use	Agriculture	− 5.8509	984.963	0.00004	− 1924.64	1936.343	<i>0.995260</i>
Land use	Urban	− 5.9314	984.964	0.00004	− 1924.56	1936.426	<i>0.995195</i>

Estimate of the effect modeled according to probability presence of *Ailanthus altissima*. Significant level for *p*-values below 0.05
 Bold values refer to significant values, *p*-values are in italics

quarter, mean temperature of the driest quarter, annual mean temperature, maximum temperature of the warmest month, mean temperature of the coldest quarter and mean temperature of the wettest quarter (Fig. 3B). Among these, the only climatic variable that explains in a significant way the presence of *Ailanthus* is the increase in the mean temperature of the warmest quarter (estimate of the effect − 2.6051; *p* = 0.019567).

Within the range of distance from the road side of 0 to 200 m, a more detailed analysis showed that the occurrence of *Ailanthus* is affected by climatic and geographical variables. In detail GLM results (Table 3) revealed that *Ailanthus* presence is negatively affected by mean annual temperature with an estimate of the effect of − 0.15247 and *p* = 0.021701). Concomitantly, elevation limits the presence of *Ailanthus* too, with an estimate of the effect of − 0.0737 and *p* = 0.037488.

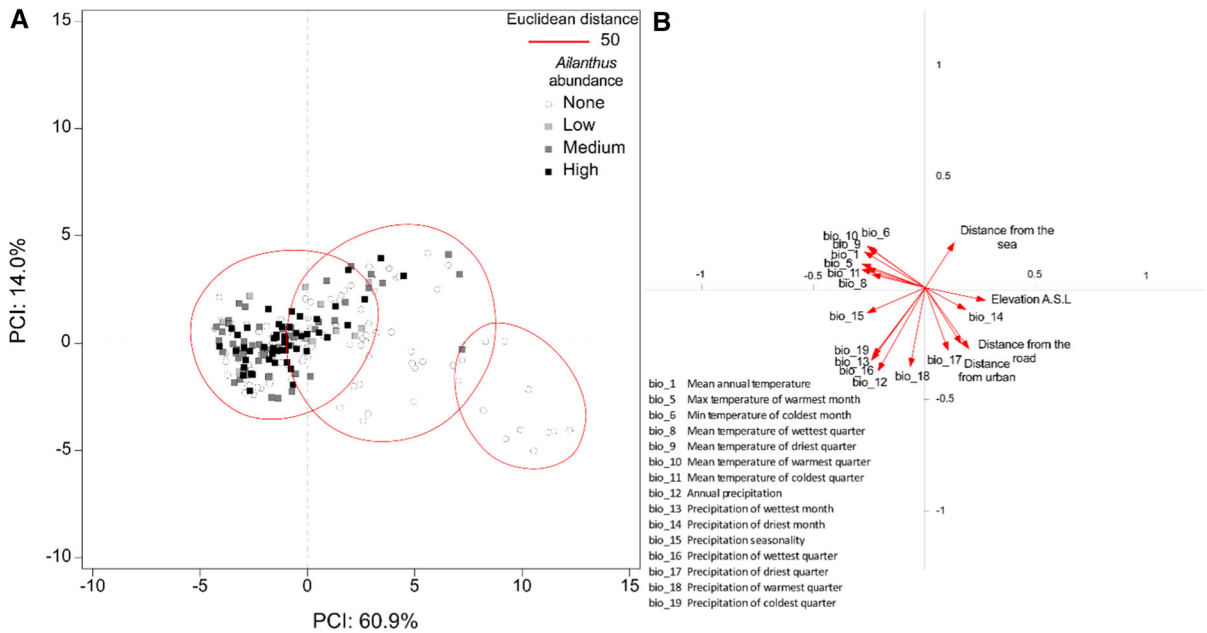


Fig. 3 Principal Component Analysis of sampling sites in the survey. **A** Loading plots show the distribution of the data according to geographical, topographical, and land use variables. Different point shapes indicated abundance of *Ailanthus altissima* in each transect. Clustering was made according to

fixed values of Euclidean distance. **B** Score plot of the variables included in the study and the contribution of each of them in segregation of sampling points according to Pearson correlation coefficients. Acronyms of climatic variables are explained in legend

Table 3 Result of Generalized linear model GLM based on Logit link function estimating significative variation in *Ailanthus altissima* occurrence in the 171 in a range of distance from Road from 0 to 200 m

Parameter estimates = occurrence
 Distribution: BINOMIAL, Link function: LOGIT
 Modeled probability that occurrence = Presence

Variables	Level of effect	Estimate	Standard error	Wald stat	Lower CL 95%	Upper CL 95%	<i>p</i> value
Intercept		27.99104	1536.961	0.000332	− 2984.40	3040.380	<i>0.985470</i>
Mean annual temperature		− 0.15247	0.066	5.269639	− 0.28	− 0.022	0.021701
Annual precipitation		− 0.00325	0.005	0.385923	− 0.01	0.007	<i>0.534450</i>
Elevation A.S.L		− 0.00737	0.004	4.328090	− 0.01	− 0.000	0.037488
Distance from the sea (km)		− 0.01295	0.015	0.703006	− 0.04	0.017	<i>0.401776</i>
Distance from urban (m)		0.00036	0.001	0.466022	− 0.00	0.001	<i>0.494823</i>
Land use	Woodland	− 0.66023	1536.904	0.000000	− 3012.94	3011.616	<i>0.999657</i>
Land use	Agriculture	− 0.43884	1536.904	0.000000	− 3012.72	3011.837	<i>0.999772</i>
Land use	Urban	1.96274	1536.904	0.000002	− 3010.31	3014.239	<i>0.998981</i>
Land use	Mixed bushes	18.59256	2330.665	0.000064	− 4549.43	4586.613	<i>0.993635</i>
Land use	Uncultivated	0.45328	1536.904	0.000000	− 3011.82	3012.730	<i>0.999765</i>

Estimate of the effect modeled according to probability of presence of *Ailanthus altissima*. Significant level for *p*-values below 0.05
 Bold values refer to significant values, *p*-values are in italics

Discussion

Climate and roads control *Ailanthus* distribution

In this study, we provided a thorough assessment of *Ailanthus* distribution in Campania. This detailed survey demonstrated that climate and anthropogenic factors interact in determining the invasive capability of *Ailanthus*. In detail, we found that climate and human-associated variables are correlated with the occurrence of *Ailanthus*, with the temperature more influential at high elevation sites, while the distance from the road plays a prominent role in low elevation areas. Our data provide evidence that the distribution of *Ailanthus* in Campania is the result of interaction between climatic factors and the road network.

Our study indicates that roads contribute to the spread of the invasive *Ailanthus*, with this species that is unable to spread in any ecosystem type when the distance exceeds 500 m from the road. Several studies have reported that roads contribute to the spread of invasive perennial herbs (Brisson et al. 2010), shrubs (Flory and Clay 2006), and trees (Zalba and Villamil 2002) in a range of ecosystems. *Ailanthus* has been reported to be common along transportation corridors in many areas around the world, and vehicles play an important role as drivers of the invasion of this species (McAvoy et al. 2012; Tyser and Worley 1992; Von der Lippe and Kowarik 2007). In this regard, our results mainly confirm previous findings, with the road that promotes the spread of *Ailanthus* in the Mediterranean climate. Indeed, although roads are known to provide more suitable habitat for exotic plants, the underlying ecological mechanisms are still not fully explained. Understanding the mechanisms by which roads promote the *Ailanthus* invasion will require further experimental studies. Here we discuss some possible explanations. First, roads provide corridors for invasion by facilitating seed dispersal (Mortensen et al. 2009). Since *Ailanthus* is a wind dispersal species with heavy seeds, corridors such as roads could be especially effective in promoting dispersal of large seeds that otherwise would have a limited dispersal capability in a closed forest. Invasion, however, depends on both propagule pressure and favorable growing conditions that determine community invasibility (Lonsdale 1999). In this regard, roads provide a suitable habitat for *Ailanthus* establishment and growth. Roadsides are subject to frequent disturbance

due to vehicle passage, periodic cleaning activities that include vegetation cutting and, sometimes, localized fire. As a consequence, roadsides may provide more resources compared to surrounding plant communities both in terms of soil nutrients and light availability (Trombulak and Frissell 2000). Recurrent disturbance decreases competition by native vegetation, leaving unused resources for potential invaders. This pattern is consistent with the fluctuating resource hypothesis, according to which an increase in unused resources promotes invasion of the plant community (Davis and Thompson 2000). Also changes in physicochemical characteristics of disturbed soils, as change of pH, water availability and increased light irradiation, could be the triggering factor, promoting germination and establishment of invasive plants (Mortensen et al. 2009). Moreover, the mechanisms of invasibility of *Ailanthus* could take into account also local mechanisms like the increase in concentration of carbon dioxide, that is characteristic of urban settlements and road sites (Davis et al. 2005). Given the fluctuation, in several physicochemical characteristics of disturbed soil (Robertson et al., 1993; Gross et al., 2005), the assessment of their effect on the invasibility of *Ailanthus* requires more detailed evaluation, probably with the help of experimental procedures. In other words, frequent disturbance facilitates fast-growing, early colonizer species like *Ailanthus*, as such species benefit from improved resource availability, compared to less disturbed vegetation. Experimental work is needed to identify the type and amount of resources that benefit *Ailanthus* along roadsides.

In contrast, we found that native pasture and woodland are especially resistant to *Ailanthus* invasion. Bonanomi et al. (2018) reported, in Campania, that canopy gaps formed by windstorms in an evergreen *Quercus ilex* urban forest are prone to *Ailanthus* invasion: the soil in gaps have higher light availability at ground level, higher mineral nitrogen content, and more moisture in topsoil compared to non-disturbed forest. *Ailanthus* is a shade-intolerant species that thrive in gaps. However, this study also highlights the importance of water availability for it to invade the Mediterranean ecosystem. The Mediterranean climate is characterized by the alternation of cold and wet (autumn–winter) and hot and dry (spring–summer) seasons. It has been widely shown that Mediterranean summer drought establishes particularly severe microclimatic conditions for the regeneration of tree

species. In such conditions, an intact forest canopy may buffer local microclimatic severity by decreasing air temperature and simultaneously increasing relative humidity, thus mitigating vapor pressure deficit and transpiration losses. Despite this, a higher soil water content in forest gaps has been recorded (Ritter et al. 2005), including in Mediterranean forests (Bonanomi et al. 2018). Higher soil moisture in the gap is likely caused by a combination of lower canopy interception (Bellot et al. 1999) and lower transpiration losses. Indeed, forest gaps in Mediterranean conditions are habitats that provide more resources and are prone to plant invasion. In this regard, roads may functionally resemble large gaps. Further experimental work is needed to clarify whether roads act as gaps in terms of resources, focusing on mineral nutrients and water availability compared to adjacent, less disturbed ecosystems. Finally, some recent studies reported that *Ailanthus* takes advantage of the association with arbuscular mycorrhizal fungi, highlighting the potential role of such beneficial microbes in facilitating plant invasion (Badalamenti et al. 2015). However, since most reported experiments were carried out under controlled conditions, further studies that investigate the difference in soil microbiome in roadsides compared to less disturbed plant communities are needed.

At a global scale, the climate is the primary factor controlling the distribution of tree species. Indeed, it has been shown that mean annual temperature and growing season temperature are key parameters to explain tree distribution along latitudinal and altitudinal gradients (Booth et al. 2016; Körner 2012). At a global scale, *Ailanthus* is a widespread invasive species in the northern hemisphere covering a broad range of climatic conditions, being more common and abundant in temperate and Mediterranean climatic zones (Walker et al. 2017). Cabra-Rivas et al. (2016) on a global scale found that *Ailanthus* prefers intermediate temperature conditions, with an annual mean temperature being the most influential variable. In this context, our study provides useful insights to assess the contribution of climatic factors in determining the current distribution of *Ailanthus*. In agreement with previous findings, our data show that *Ailanthus* prefers mild climates, with altitudinal distribution limited by low temperature. In our survey, the highest occurrence of *Ailanthus* was at 870 m a.s.l.. The mean annual temperature of 11.1 °C at this elevation poses a

climatic constraint upon the distribution of this species. Further, we found that the distribution of *Ailanthus* is positively correlated with mean annual temperature, as well as with temperature in the warmest and coldest quarter. In this regard, our correlative approach cannot identify whether *Ailanthus* is more limited by cold winters or low temperatures during the growing season. Interestingly, *Ailanthus* has peculiar phenology, being characterized by late flush and flowering in spring (Castro-Diez et al. 2014) and an early leaf fall in autumn compared to deciduous native species, i.e., *Fraxinus ornus*, *Ostrya carpinifolia*, *Populus nigra*, *Quercus pubescens*. The short growing season of *Ailanthus* could be adaptive at low elevation to reduce the risk of frost damage in spring (Allevato et al. 2019), but could also limit the ability of this species to colonize cold climates because the growing season could be too short to achieve a positive carbon budget. Further eco-physiological studies are needed to identify the factors that limit the spread of *Ailanthus* in cold climates.

Alongside temperature, precipitation also affects the global distribution of *Ailanthus*, with the species absent in arid climates (Walker et al. 2017). Although *Ailanthus* is considered a drought-tolerant tree thanks to its extensive root system and specific metabolic pathways (Filippou et al. 2014), it does not grow in areas with pronounced droughts (Walker et al. 2017). In our study, *Ailanthus* was poorly correlated with precipitation-associated variables. In Campania rainfall follows a typical Mediterranean pattern with summer drought. Yet annual rainfall often exceeds 1,000 mm per year, even in coastal areas and at low elevations. Therefore, our data indicate that rainfall is not a limiting factor for the spread of *Ailanthus* in Campania.

Conclusions and management implications

Effective management of *Ailanthus* invasion requires precise determination of favoring and limiting plant spread factors. This study showed that in the southern Italian region of Campania the climate is suitable for *Ailanthus* in terms of temperature and rainfall, with the only major limitation being the temperature at an altitude exceeding 900 m a.s.l. Moreover, roads emerge as the primary landscape feature along which this species spreads and invades new areas. At present, *Ailanthus* is widespread and an eradication program

appears prohibitive in economic terms. In addition, the only effective method is the combined use of mechanical removal and herbicide application (Constán-Nava et al. 2010), posing a major doubt about the ecological sustainability of such an approach. Environmental managers must focus on avoiding a further extensive spread in natural environments, including pasture, shrubland, and forests. Identification of ecological factors that confer resistance of the plant community to biological invasion would provide useful insights to draw up effective guidelines for managing *Ailanthus*.

Author contributions RM, and GB conceived and designed the experiments. RM, AC, and AS collected Data. MZ, AM, and GB analyzed the data. RM, AM, MZ, and GB wrote the manuscript.

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