Exploring cross-taxon congruence between carabid beetles (Coleoptera: Carabidae) and vascular plants in sites invaded by *Ailanthus altissima* versus non-invaded sites: the explicative power of biotic and abiotic factors

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Abstract

Ailanthus altissima is one of the most global widespread invasive alien species and its effect as habitat transformer requires detailed investigations. In particular, its invasion in natural ecosystems and its effect on local fauna should be evaluated and described. With this purpose, the identification of surrogate taxa would be an important tool in order to define the impact of this invader on different habitats. Here, we evaluated cross-taxon congruence to quantify the strength of plant species composition in predicting multivariate patterns in carabid beetle assemblages, based on data from 20 sites divided in invaded and non-invaded habitats located in the Karst area, North-east Italy. We considered the habitat type (representing vegetation stages from grassland to forests) in order to evaluate the impact of *A. altissima* on carabid beetles along the vegetation succession. We found 28 carabid beetles and 173 plant species. Our analyses showed that plant species composition had a valuable predictive accuracy, based on the interplay among environmental variables, soil parameters and vegetation structure. Native vegetation and habitat type were the most important factors influencing carabid beetles and plant species composition. Furthermore, 33% of the total explained variation of carabid beetles assemblages (variance partition based on RDA analysis) was due to the independent effect of environment. We proved cross-taxon congruence between carabid beetles and plants along the successional gradient of vegetation (habitat type). In particular, we attested that both communities present more species differentiation among non-invaded vegetation

and, in the meantime, in plots were *A. altissima* was present, anthropic and disturbed plants and carabid beetles species were prevalent. As a conclusion, plants can be effectively used as a surrogate taxon in the evaluation of the effect of *A. altissima* invasion in the Karst area.

Keywords

Carabidae; Co-correspondence analysis; Invasive species; Plant community; Surrogate taxon; Variation partitioning.

1. Introduction

The study of non-native species (or exotics; Sax, 2002a, 2002b; Hejda et al., 2009) became very popular in the last twenty years (Briggs, 2013; Díez et al., 2014; Tordoni et al. 2018), and recently this field underwent an important shift in research priorities (Pyšek, 2008). In fact, the impact of introduced species outside their native range by human-mediated activities or disturbances is increasing in an era of globalization (Grigorescu, 2016). The heart of invasion science is the realization that biological invasions are not only a biological phenomenon: the human dimension of invasions is a fundamental component in the social-ecological systems, in which invasions need to be understood and managed (Wilson et al., 2016). Several studies highlighted how invasive alien species (hereafter IAS) may threat human well-being (Schlaepfer et al., 2010) as well as affect natural ecosystems in several ways (see Vilà et al., 2011 for a meta-analysis); for instance, it has been observed that IAS may cause loss or modification of biological diversity (Hejda et al., 2009), modifying also native species extinction probabilities, and habitat structure (Blackburn et al., 2014).

A detailed knowledge of the biology and ecology of individual invasive species is an important tool in the quest for a better understanding of invasion phenomena (Pyšek, 2008) but unfortunately, for the vast majority of non-native species, the consequences of invasion are not yet fully understood (Jeschke et al., 2014) or realized (the so-called 'invasion debt', Rouget et al., 2015).

An important subset of IAS comprehends tree species able to form mono-specific stands in invaded areas, and that are therefore major drivers of environmental change (Richardson, 2011). One of the most important global colonizing tree is *Ailanthus altissima* (Mill.) Swingle (Kowarik and Saümel, 2007; Motard et al., 2011; Sladonja et al., 2015). *A. altissima* is a deciduous tree native to China that belongs to the *Simaroubaceae* family. It arrived in Europe at the mid-XVIII century in Paris (Enescu et al., 2016). Thanks to its fast expansion, it is considered as invasive in the most part of

Europe (Motard et al., 2011; Petruzzellis et al. 2019a,b), and it is cited as a concern for biodiversity according to the Global Invasive Species Database (GISD, 2017). The first reason of this tree success is the vegetative reproduction ability in forming dense clonal stands; the second reason is the sexual reproduction. The species is common not only in disturbed urban and anthropic areas (Vila et al., 2006; Motard et al., 2011; McAvoy et al., 2012; Motard et al., 2015; Enescu et al., 2016), but can also penetrate forests (Motard et al., 2011). *A. altissima* produces allopathic compounds and has an insecticidal activity (Tsao et al., 2002; Motard et al., 2011 and 2015; Enescu et al., 2016); moreover, its pollen is allergenic (Ballero et al., 2003). It has been shown that this species can rapidly transform open ecosystems such as meadows or old fields into closed stands (Kowarik and Böcker, 1984; Kowarik and Saümel, 2007) promoting impoverishment of biological diversity through competition (Motard et al., 2011). Moreover, it spreads and displacesnative vegetation thanks to a huge canopy cover and due to a large amount of root suckers; its allelopathy results in a significant lower floristic diversity respect to native adjacent zones (Motard et al., 2011). An earlier study in forests colonized by *A. altissima* suggests that an increasing density of this plant is associated also with a lower soil microbial activity, with decreasing abundance of Acari, Collembola, Coleoptera, and terrestrial Gastropoda. Contrarily, increasing *A. altissima* density is linked to greater abundances of Lumbricidae and coprophagous Coleoptera (Motard et al., 2015). However, it is still unclear whether this impact is due to the direct action of *A. altissima* by phytotoxicity of the root system, or to the transformation of soil and litter fauna (Motard et al., 2011).

Due to the lack of information concerning the impact of *A. altissima* on terrestrial arthropods, we addressed the issue of the impact of this tree on carabid beetles (Coleoptera, Carabidae) assemblages in different open to forested habitats.

The importance of Invertebrates as bioindicators in conservation planning (Kremen et al., 1993; McGeoch, 1998; Andersen et al., 2002; Hodkinson and Jackson, 2005) is well known, since they are ubiquitous, a taxon-rich and dominant group of organisms throughout the world (Wilson, 1987). The carabid beetles represent the fourth largest family in Coleoptera (Löwei and Sunderland, 1996). Carabids are a group of Insects with terrestrial habits (Löwei and Sunderland, 1996; Koivula et al., 1999; Moraes et al., 2013) mainly characterized by carnivorous species (Marinoni et al., 2001; Marinoni, 2001), even though omnivorous exceptions are known for some tribes (Talarico et al., 2016). Due to their adaptations, ecological requirements rather than habitat features have been claimed to influence carabid communities; in fact, in this group, structural features may be suitable or adapted to perform in several different habitats (Ribera et al., 2001). Most carabids are relatively long-lived, and many species do not show any strong seasonal fluctuations, allowing useful sampling activities, performed using pitfall traps (Desender et al., 1994; Luff, 1975; Lee and Albajes, 2016), to be carried out in relatively short periods (Lindroth, 1974; Ings and Hartley, 1999). For these reasons, they represent an important and suitable study group in ecological research, especially for what concerns standardized samplings (Lee and Albajes, 2016; Zhang et al., 2017). Studies concerning carabids have addressed their diversity as indicators in distinct topics, for example: effect of environmental modifications (e.g. Thiele; 1977; Niemelä et al., 1993; Lövei and Sunderland, 1996; Villa-Castillo and Wagner, 2002; Kotze et al., 2011), environmental integrity (Taylor and Dorann, 2001); disturbance gradients (da Silva et al., 2008), effects of alien species (Martínez et al., 2009; Buchholz et al., 2015). Vascular plants can be potentially considered a good proxy for invertebrates and have been widely used for this purpose due to their well-known ecology, their relatively ease in identification, and sensitivity to environmental changes (e.g. Sætersdal et al., 2003; Schaffers et al., 2008; Gioria et al., 2010; Maccherini et al., 2012).

The diversity of different taxa is influenced by their spatial concordance and by the strength of this association, the so-called cross-taxon congruence, which depends on the studied taxonomic groups, on the scale of analysis (Toranza and Arim, 2010) and on the type of data used (Santi et al., 2016). Cross-taxon congruence analysis can be a suitable tool to elucidate spatio-temporal correlation in patterns of species richness and/or diversity of organisms using surrogate taxa as potential biodiversity indicators (e.g. Margules and Pressey, 2000; Sætersdal et al., 2003). In this way, environmental parameters could be effectively used and potentially also be directly managed in the context of biodiversity conservation to make biodiversity monitoring and conservation planning more efficient (Su et al., 2004; Oertli et al., 2005; Gioria et al., 2011; Barbato et al., 2019). Thus, surrogate taxa could be identified based on the direct biotic interactions such as trophic relationships between target and surrogate taxa (Castagneyrol et al., 2012; Westgate et al., 2014).

Generally, cross-taxon congruence is well-connected with similarities in the response patterns of taxa to changes in environmental gradients, biotic interactions or even in their biogeographical history (Pearson and Carroll, 1999; Su et al., 2004; Duan et al., 2016). Despite some criticisms (e.g. Westgate et al., 2014), the use of surrogate taxa to predict community patterns remains a very useful tool especially in case of limited resources or if knowledge gaps make difficult a complete species inventory. It should be also considered that cross-taxon congruence can be promoted by longer disturbance gradient, increasing species characteristic of low or high disturbance levels (Rooney et al., 2014). Nonetheless, the relative contributions of environmental abiotic drivers and biotic interactions in cross-taxon congruence still remains widely unknown (Gioria et al., 2011).

In this study, we aimed at evaluating the impact of *A. altissima* invasion on carabid beetles species composition and assessing the role of vascular plants as a possible surrogate group for the distributional and diversity patterns of carabid beetles in North Adriatic Karst (hereafter NAK). Furthermore, the joint and independent effects of spatial location, abiotic variables, non-invaded and invaded vegetation structure, have been also tested to understand their explanatory role in shaping the observed congruence patterns. Specifically, we aimed at: (1) assessing cross-taxon congruence between carabid beetle and vascular plant compositions along a successional gradient of vegetation (from grassland to forest) in sites invaded and non-invaded by *A. altissima*; (2) quantifying and comparing the ability of vegetation structure and environmental variables to predict carabid beetle species composition in both non-invaded and invaded habitats. Additionally, we supposed that cross-taxon congruence between carabid beetles and plants differ among non-invaded and invaded sites; particularly, in invaded sites we expected more homogenous communities all along the successional gradient of vegetation. More, we hypothesized that *A. altissima* favors more synanthropic and euriecious carabid beetle and plant species.

2. Materials & methods

2.1. Study area

Fieldwork was carried out in the northeastern part of Italy, in North Adriatic Karst (NAK). The study area (total extension of 4.9 km^2) ranges between 58-114 m a.s.l. and lies in the municipalities of Ronchi dei Legionari and Doberdò del Lago (Fig. 1). The NAK is a well-known area for its geographical and geomorphological characteristics, located between the Adriatic Sea and the Alps. The study area encompasses the westernmost part of the Italian Karst, that consists of the limestone plateau (100-500 m a.s.l.), characterized by the typical geomorphological karst phenomena (karst poljes, dolines, caves, etc.), and Red Mediterranean soils (Kaligarič et al., 2006; Poldini, 2009).

The Karst is known and traditionally recognized as a treeless, stony grassland landscape (with exceptions of many flysch-bedrock patches), where the strong and cold Bora wind affects vegetation causing desiccation and soil erosion. The climate is sub-Mediterranean, transitional between Mediterranean and continental pre-Alpine types, with rainy cool winters and long and relatively dry summers (Kaligarič et al., 2006; Poldini, 2009).

Currently, Karst landscape is generally dominated by mixed deciduous termophilous woodlands of *Quercus pubescens*, *Ostrya carpinifolia* and *Fraxinus ornus*.

In the study area, we have identified one successional gradient of vegetation typical of the calcareous soils of the Karst plateau: in phytosociological term, the vegetation series belong to the series leading to the thermophilous mixed oak woods dominated by *Quercus pubescens* (*Aristolochio luteae-Quercetum pubescentis* (Horvat 1959) Poldini 2008)). Along this dynamic series of vegetation, we have selected non-invaded and invaded by *A. altissima* stages.

For methodological simplicity, each successional stage of the Karst vegetation series was defined as an habitat due to homogeneous vegetation characteristics. In total 4 different habitats were identified and sampled, of which four were not invaded (coded as 1, 2, 3 and 4) and three were invaded by *A. altissima* (coded as 5, 6 and 7). Within each habitat, three randomly selected plots (of almost 500 m^2 each) were sampled where both carabids and vegetation were investigated following the scheme described below. It follows a brief description of the habitats along with the definition of sampled plot codes.

Non-invaded communities (4 habitats):

(1) *Karst grassland*: characterized by *Centaureo cristatae-Chrysopogonetum grylli* Ferlan and Giacomini 1955. Thermoxerophilous dry grassland (*A. altissima* absent). Here three plots were sampled and coded as KG1, KG2, KG3.

(2) *Karst bushes (shrubland)*: this habitat is characterized by thermoxerophilous shrubs (*A. altissima* absent) belonging to *Frangulo rupestris-Cotinetum coggygriae* Poldini and Vidali 2002 association. Three plots coded as KB1, KB2, KB3 were sampled.

(3) *Karst Wood in doline (dolines)*: characterized by mixed deciduous *Quercus pubescens* woodland in shallow dolines (native species abundance > 90%, *A. altissima* < 1%). Three plots coded as KW1, KW2, KW3 were sampled.

(4) *Karst Quercus woodland*: this habitat is characterized by *Aristolochio luteae-Quercetum pubescentis* (Horvat 1959) Poldini 2008. Mature woodland of *Q. pubescens* (*A. altissima* absent). Three plots coded as KQW1, KQW2, KQW3 were sampled.

Invaded communities dominated by *A. altissima* (3 habitats):

(5) *A. altissima* on karst grasslands: this habitat represents the first step of *A. altissima*'s colonization on dry calcareous grassland (*A. altissima* abundance > 60%, native species abundance < 20%). At the beginning of the study three plots were individuated, but one was destroyed by fire. Therefore, two plots coded as AG1, AG2 were sampled.

(6) Bushland with *A. altissima*: characterized by the phases of invasion of *A. altissima* in karst shrublands and pre-woods (*A. altissima* abundance > 55%, native species abundance < 35%). Three plots coded as AB1, AB2, AB3 were sampled.

(7) *A. altissima* Wood: represented by dense and monospecific *A. altissima* woods in shallow dolines (*A. altissima* abundance > 90%, native species abundance < 5%). Three plots coded as AW1, AW2, AW3 were sampled.

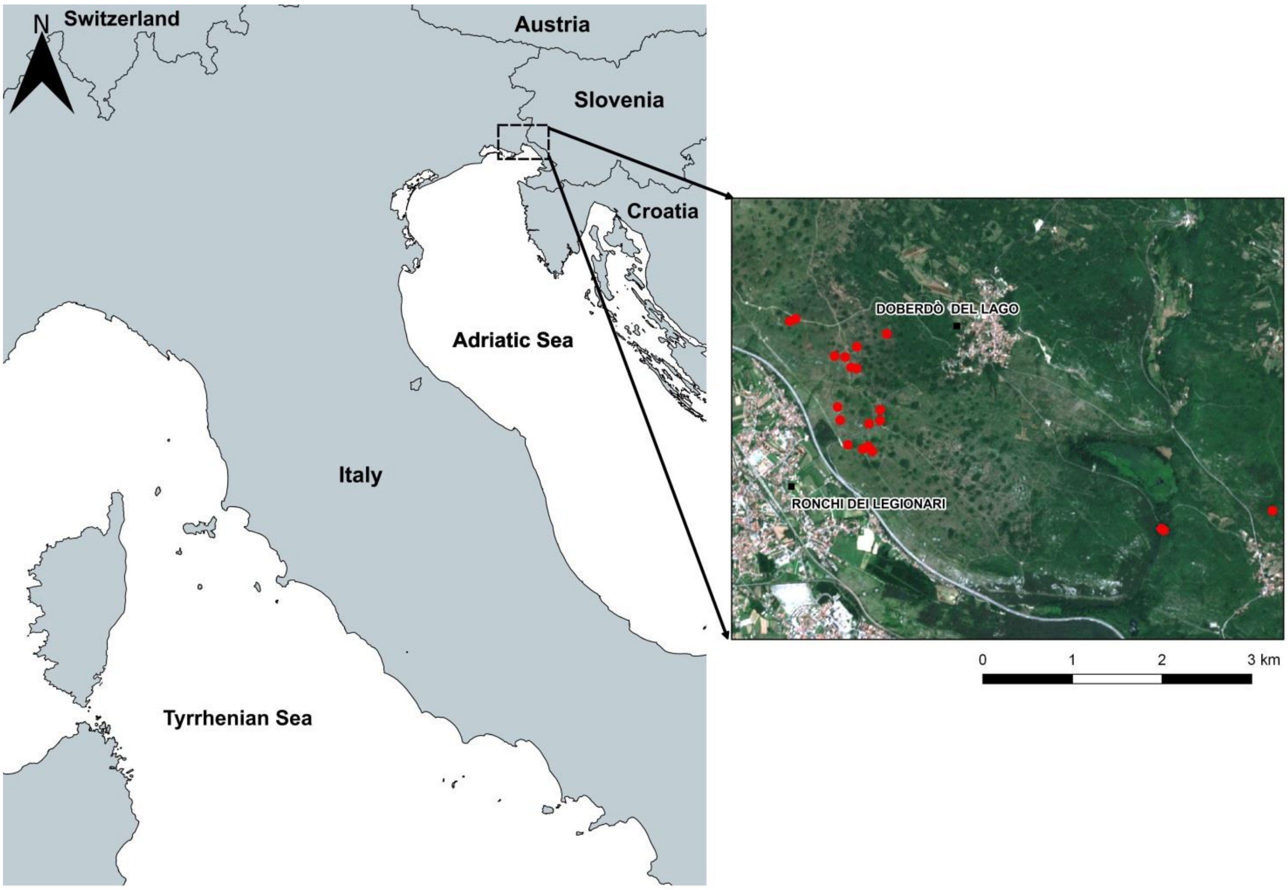

Fig. 1. Study area with respect to Italian peninsula (left panel); the right panel shows a particular of the study area highlighting the sampled plots and the two municipalities near the study areas (Ronchi dei Legionari and Doberdò del Lago; Friuli Venezia Giulia region) (aerial photo from IRDAT FVG, http://irdat.regione.fvg).

2.2. Carabid beetles sampling

In each plot, three pitfall traps were placed 10 m apart in a straight line at the center of the area (N-W direction). The pitfall method is considered an inexpensive and labour efficient way to collect carabids for statistical analysis (Capar, 2003). Following Brandmayr et al. (2005), Zhang et al. (2017) traps were made by plastic vessels with an upper diameter of 9 cm and a depth of 11 cm provided with two small holes to avoid water filling and "aquaplaning effect" of beetles. Traps were filled up to two thirds of their depth with wine-vinegar saturated by sodium chloride as further preservation measure. Vinegar has been demonstrated to be a good collecting fluid and compared to pure water it allows a collection of larger numbers of species and individuals by avoiding degradation of anatomical structures (Mazzei et al., 2015). Carabid beetles were collected from 10th May 2014 until 12th January 2017 with a monthly control and emptying of pitfall-traps all year round. The activity density of each species was calculated as DAa (annual activity density) expressed as individuals/trap in the standard period of 10 days, the captures of all species as ADat (total annual activity density) as in Brandmayr et al. (2005).

2.3. Vegetation data collection

In the central part of the 20 plots, an area of 10 m x 10 m was sampled. Within it, vascular plant occurrences and abundances were recorded. Abundance was evaluated as percentage cover, expressed using a seven-point scale according to Braun-Blanquet (1964). Sampling was carried out in May-June 2014 and August-September 2014 in order to get a complete composition of plant communities.

2.4. Vegetation structure analysis

In each of the 20 plots, we randomly defined a quadrat of 100 m^2 where we measured the following metrics only for woody species higher than 1 m: *mean height* (H_mean), *mean diameter* (D_mean), *mean total number of trees* (N), *density* and *total percentage cover* (Cop) of woody indigenous tree species (I) and for *A. altissima* (A). The diameter was calculated at breast height (DBH) using a metal tree caliper and the resulting measure was the arithmetic mean of the two readings, according with Clark et al. (2000). The estimate of the tree height was performed using a manual hypsometer, a precise and fast instrument (Rennie, 1979) using geometrical and trigonometric principles to determine tree height.

2.5. Soil parameters

A soil pit 10 cm x l0 cm x l0 cm was dug near the center of the 20 plots. To characterize soil properties, we considered the following variables: *soil rock fragments, soil fine earth fraction, soil fine earth fraction, soil humidity, soil bulk density, soil porosity, soil mean weight diameter* (Table A.1 in Appendix A in Supplementary material). One sample was taken from the upper part of the mineral soil (0-7 cm in KG, AG, KB, 0-10 cm in KQW, 0-8 cm in AW, AB and KW) on each plot in October 2017. The soil bulk density is the mass to volume ratio of an oven-dried soil. It was determined in the 0-10 cm surface soil layer of all investigated sites, following the methods described by Grossman and Reinsch (2002). In non-gravelly soil surface strata, it was determined with the core method by using a steel cylinder of 10 cm height and 0.724 l volume. The cylinder was inserted in the soil with the help of a steel hammer with nylon heads and dug out with a shovel. The soil sample was finally extracted from the cylinder and put in a plastic bag. When the content of rock fragments was high, an alternative excavation method was adopted. A plastic film with a central hole of 15 cm diameter was placed on a roughly plain soil surface. A soil sample was dug out of the hole with a knife, put on the plastic film and transferred in a plastic bag. Afterwards, the excavated hole was covered with a second plastic film and filled with water to the surface with the help of 250 ml graduated cylinder. The volume of the hole was given by volume of water added to the excavated hole. In both cases, samples were transported in the laboratory, oven-dried at 105°C and weighted. The bulk density was calculated as the mass to volume ratio of oven-dried cores and expressed as kg L-1. Total soil porosity was obtained by the equations:

$$\text{Total porosity} = 1 - \rho a / \rho s$$

where ρa is the bulk density, and ρs the particle density of the soil, which usually averages 2.65 Kg l-1. Soil porosity was obtained from soil bulk density; soil mean weight diameter refers to the mean dimension of soil aggregates; soil fine earth fraction is the solid fraction less than 2 mm.

2.6. Environmental variables

We derived environmental variables (Latitude, Longitude, Slope, Elevation, Northness, Eastness, depth of dolines) from the Digital Elevation Models (DEMs, resolution 10 m) using ArcGIS 10.2.1 (ESRI, 2014). Karstification level was defined following Forti (1982).

Plot environmental characteristics (ordered by successional gradient of vegetation from wood to grassland) are reported in Table A.2 in Appendix A in Supplementary material.

2.7. Statistical analysis

Cross taxon congruence between plants and carabid beetles and their relationships with the other predictors were assessed using different statistical methods. Firstly, Mantel and partial Mantel test were calculated using Spearman correlation coefficients and 999 permutations. This analysis aims at assessing the significance of the relationship between pairwise distance of species composition (both carabids and plants) and those of predictor variables (Legendre and Legendre, 2012; Frenett et al., 2013; Westgate et al., 2014; Larios et al., 2017). Before performing Mantel and partial Mantel test, distance matrices for each group of variables (environmental parameters, soil parameters, vegetation structure; Fig. A.1 in Appendix A in Supplementary material) were calculated as follows: 1) for environmental variables, soil variables and vegetation structure, a Euclidean distance matrix was calculated; 2) for carabid beetles and plant communities the Bray-Curtis distance was used (Legendre and Legendre, 1998). Carabid abundance data and plant community data were square root transformed prior to analysis to meet assumptions about normality**.** Later, Co-correspondence analysis (Co-CA, see ter Braak and Schaffers, 2004; Schaffers et al., 2008 for a full description of this method), was used to quantify the strength of plant community data in predicting the carabid beetle species composition. Here, we used the predictive version of Co-CA, which combines the maximization of weighted covariance between weighted averages of species scores and partial least squares methodology (PLS; Martens and Naes, 1992). A leave-one-out cross-validatory fit percentage was estimated to select the minimal adequate predictive models. Schaffers et al. (2008) pointed out that, due to its predictive nature, any cross-validatory fit > 0 implicitly validates the model, indicating that prediction is better than that obtained under the null model. A permutation test for predictive co-correspondence analysis models to assess the significance of each Co-CA ordination axis was applied (999 permutations); in addition, abiotic and biotic vectors were fitted onto ordination axes assessing the importance and significance of each vector by means of '*envfit.coca*' function.

In order to further assess the relationships between beetles and successional stages of vegetation, we used indicator species analysis (Dufrêne and Legendre, 1997) coupled with combinations of site groups according to De Cáceres and Legendre (2009). The same analysis was also applied to detect differences between non-invaded *vs.* invaded stages of vegetation.

Lastly, the pure and shared effect of spatial factors, soil and environment parameters, vegetation structure on plants and on carabid communities was evaluated using a variation partitioning approach that allows the partitioning of the total variation (calculated as partial redundancy analysis) to be broken down into the contributions of each variable group (Borcard et al., 1992; Peres-Neto and Legendre, 2010).

Mantel and partial Mantel tests along with variation partitioning were computed using R package *vegan* (Oksanen et al., 2018); Co-CA and related analysis with R package *cocorresp* (Simpson, 2009), indicator species analysis with R package *indicspecies* (De Cáceres and Legendre, 2009). All statistical analyses were performed using R 3.5.1 (R Core Team 2018).

3. Results

In total, 3119 individuals were collected belonging to 28 carabid species. Non-invaded stands (KQW2) showed higher abundance of carabids whereas values of invaded stands the lowest ones (AG2; see Table A.2 in Appendix A in Supplementary material). Overall, the most common species was *Carabus coriaceus coriaceus* and the rarest were *Carabus granulatus interstitialis*, *Harpalus serripes*, *Ophonus azureus*, *Brachinus explodens*. Invaded wood was the habitat type where the highest number of species was detected (15 species in AW3, 11 species in AW1); in contrast, non-invaded karst bushes showed lower values of carabid species richness (2 species in KB3) (Table A.2 in Appendix A in Supplementary material). Out of the 18 species sampled in the non-invaded and invaded wood habitats, *Laemostenus cavicola* and *Carabus granulatus interstitialis* were found only in the invaded plots, *Abax parallelepipedus subpunctatus*, *Calosoma sycophanta*, *Notiophilus rufipes* were found exclusively in non-invaded woods. In total, 10 species were associated only with *A. altissima*: *Licinus hoffmanseggii, Abax carinatus sulcatus, Carabus catenulatus catenulatus, Harpalus atratus, Leistus rufomarginatus, Harpalus rubripes, Ophonus azureus, Calathus melanocephalus, Brachinus explodens, Pseudoophonus rufipes*.

Considering plant species, we detected 173 species in total (mean number of species per plot was 28.55±9.35). The most abundant tree species was *Fraxinus ornus* (85% of the plots), the most abundant shrub species was *Cotinus coggygria* (70% of the plots), and the most abundant herbaceous species were *Brachypodium rupestre* (55% of the plots), *Sesleria autumnalis* (40% of the plots), *Carex humilis* (40% of the plots). As expected, non-invaded grasslands showed the highest values of plant species richness whereas non-invaded shrubs the poorest ones. 35 species were associated only with *A. altissima*, the most abundant were: *Duchesnea indica* (10% of the plots), *Elymus repens* (10% of the plots), *Erigeron annuus* (10% of the plots), *Aristolochia clematitis* (5% of the plots), *Fragaria viridis* (5% of the plots), *Mercurialis perennis* (5% of the plots), *Allium vineale* (10% of the plots), *Lathyrus latifolius* (5% of the plots), *Populus nigra* (5% of the plots). 72 species were present only in non-invaded plots: *Sesleria autumnalis* (40% of the plots), *Quercus pubescens* (30% of the plots), *Cornus mas* (25% of the plots), *Chrysopogon gryllus* (15% of the plots), *Stipa eriocaulis s.l.* (15% of the plots) *Quercus cerris* (10% of the plots).

The correlation between the plants and carabid beetles dissimilarity matrices and each group of the environment variables (e.g. soil variables, vegetation structures, habitat types distance matrices) were significant (Table 1). Even though most of the Mantel tests showed significant correlations, partial Mantel revealed that most of the cross-taxon congruence is controlled by abiotic and biotic predictors; interestingly, the correlation remained significant only after controlling for *A. altissima* presence and structure. A slight trend was detected, albeit not significant, when controlling for soil variables.

Test	**Distance matrices**	**Spearman's ρ**	**p-value**
	Plant ~ All Environment and Vegetation	0.51	**<0.001**

Mantel Test	Plants ~ Environmental Variables	0.24	**0.008**
	Plants ~ Soil Variables	0.22	**0.0123**
	Plants ~ Ailanthus presence and structure	0.22	**0.027**
	Plants ~ Native Plant Structure	0.42	**<0.001**
	Plants ~ Habitat Type	0.45	**<0.001**
	Beetles ~ All Environment and Vegetation	0.43	**<0.001**
	Beetles ~ Environmental Variables	0.40	**<0.001**
	Beetles ~ Soil Variables	0.43	**<0.001**
	Beetles ~ Ailanthus presence and structure	-0.09	0.768
	Beetles ~ Native Plant Structure	0.35	**<0.001**
	Beetles ~ Habitat Type	0.34	**0.001**
	Plants vs. Beetles	0.23	**0.019**
Partial Mantel Test	Plants vs. Beetles ~ All Environment and Vegetation	0.00	0.468
	Plants vs. Beetles ~ Environmental Variables	0.14	0.085
	Plants vs. Beetles ~ Soil Variables	0.14	0.074
	Plants vs. Beetles ~ Ailanthus presence and structure	0.25	**0.010**
	Plants vs. Beetles ~ Native Plant Structure	0.09	0.178
	Plants vs. Beetles ~ Habitat Type	0.08	0.193

Table 1. The Spearman correlation coefficients of Mantel test and Partial Mantel tests between all environmental distance matrices and the dissimilarity matrix of carabid beetles and plants (~ means: controlling for). In bold the significant values.

The ordination diagram of Co-CA analysis shows a gradient based on vegetation structure (grassland, shrubland, woodland in dolines) that could be identified along the first axis (Fig. 2). The biplot allowed the identification of thermophilous and xerotolerant carabid beetle species, typical of open habitats such as *Harpalus serripes*, *Harpalus dimidiatus, Philorhizus crucifer confusus, Poecilus koyi goricianus*, grouped on the bottom left of the diagram, and associated with the characteristic grassland plant species as *Bupleurum veronense* and *Chrysopogon gryllus*. Non-invaded mature stands dominated by *Quercus pubescens* (KQW) were all grouped together on the bottom right, and were associated to *Abax parallelepipedus subpunctatus*, *Notiophilus rufipes*, and with higher abundances of *Calosoma sycophanta, Molops ovipennis istrianus*, *Carabus catenulatus catenulatus.* These species were consistently associated with plant species typical of Karst mature forests (such as *Quercus pubescens, Quercus cerris, Asparagus tenuifolius*). In the upper part of the biplot, species connected with non-invaded and invaded stands in dolines occur: humid forest species, such as *Licinus hoffmanseggii* and *Abax carinatus sulcatus,* troglophilous and crevice dweller species *Laemostenus cavicola* and *Laemostenus elongatus*, species usually linked with swampy forests as *Carabus granulatus interstitialis,* and woodland thermophilous species as *Synuchus vivalis* and *Harpalus atratus*. In association with these carabid species there were

Lonicera caprifolium, *Lamium orvala* and *Brachypodium sylvaticum*, which are particularly abundant in doline wooded habitats.

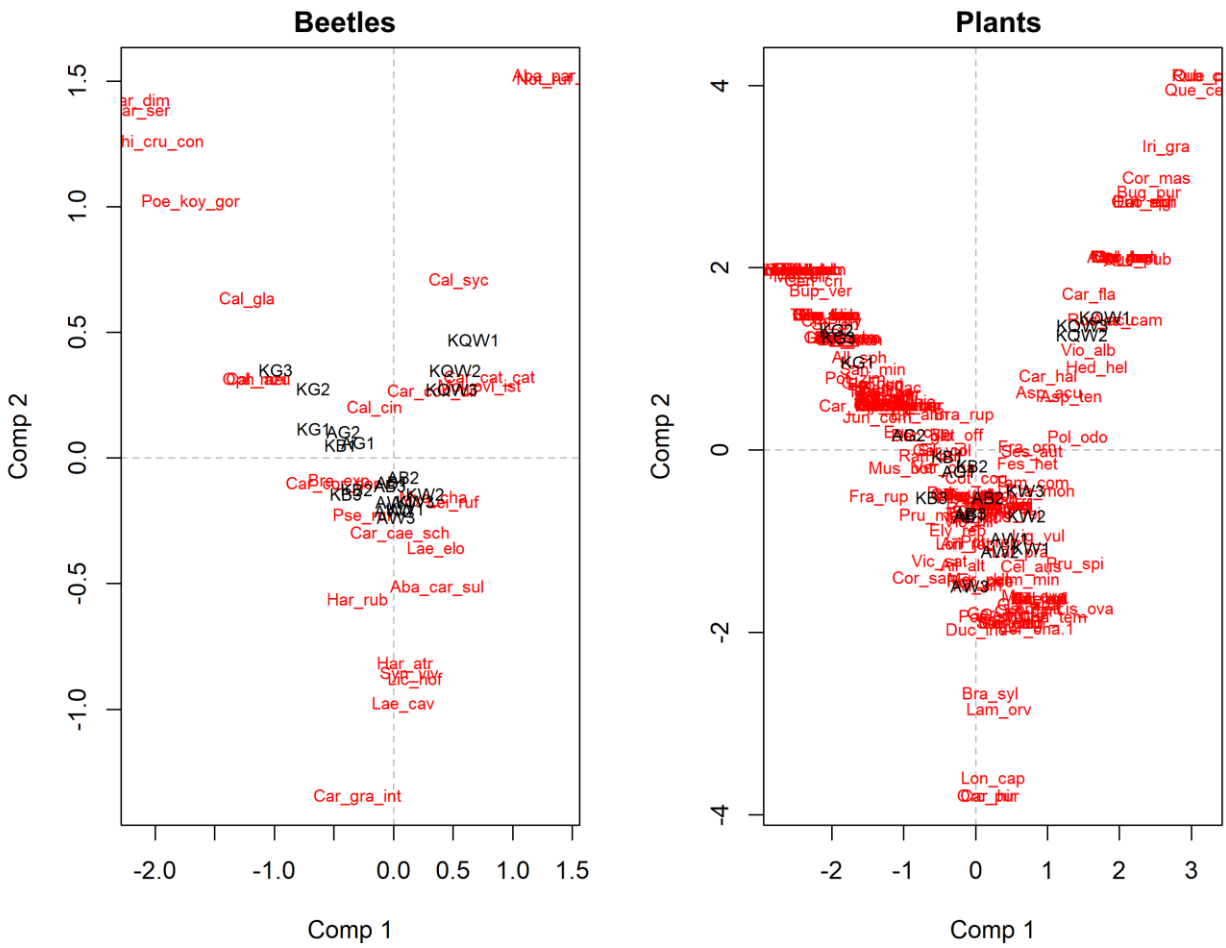

Fig. 2. Predictive Co-CA biplot of carabid beetle species composition (beetles, left) and plant species composition (plants, right) (A). In each plot, species are positioned according to their loadings with respect to normalized site scores derived from the plant composition data. The axes were rescaled to the same ranges so that sites occupy the same position in both plots.

It is very important to underline that the variables that produce an effect on congruence across taxa were the structure of non-invaded vegetation and habitat type, while invaded vegetation did not show an influence on carabid beetles and plants.

The prediction accuracy of plant species composition on beetle composition was above zero (cross-validatory fit percentages, Table 2), indicating that the predictions of carabid beetle species composition based on that variables were better than those expected under the null model (no relationship). Plotting the cross-validatory fit percentage for the compared predictive datasets against the number of axes showed the maximum prediction level obtained at three axes. In the model we therefore retained only the first axis. In Fig. A.2 in Appendix A in Supplementary material are displayed the results of the Predictive Co-Ca. These showed a clear clustering of habitat types in some groups: firstly, woods growing in dolines (both non-invaded and invaded) are characterized by higher karstification values, higher soil porosity and soil fine earth fraction; whereas *Karst Quercus woodland* are correlated with higher values of soil rock fragments and soil bulk density. All plots with the highest density of *A. altissima* are clustered together. Most of the environmental variables were significantly correlated with Co-Ca axes (Table 3). It is important to underline that we found a strong correlation of carabid beetles with soil porosity (P < 0.01), karstification (P < 0.01), non-invaded vegetation structure canopy cover (P < 0.01). Plants were strongly correlated with soil porosity (P < 0.01) and soil rock fragments (P < 0.01), karstification (P < 0.001), native canopy cover (P < 0.001), native plants diameter (P < 0.01) and native plants height (P < 0.01), diameter (P < 0.01) and height (P < 0.01).

	Predictive Power (plants on beetles)	**Cumulated Predictive Power**	**Cross-validatory fit (%)**	**p-value**
Axis 1	18.642	18.642	9.739	0.001
Axis 2	10.844	29.486	16.796	0.472
Axis 3	10.222	39.709	17.862	0.625
Axis 4	6.890	46.599	14.745	0.837

Table 2. Predictive power of plants on carabid beetles composition

Considering indicator species analysis, we found a low number of carabid beetle indicator species connected with certain successional vegetation stages. Furthermore, even though in non-invaded stages no species were detected as indicators, one species (*Calathus cinctus*) resulted as closely associated with invaded communities (Tab. A.3 in Appendix A).

The contribution of space, environment, soil parameters and vegetation structure differed between carabid beetle and plant community composition (Fig. 3). The relative contribution of spatial factors was similar between these two groups, and environmental relative contribute was the most important factor in both groups, even though beetles resulted to be more influenced (Fig. 3a,b). The relative contribution of the vegetation structure and soil factors was not coincident among the two groups. The covariation of vegetation structure with soil parameters accounted for much of the variation in plant communities. Spatial and vegetation structure factors together determined the abundance and distribution of plant pattern almost like spatial, vegetation, environment and soil together. On one hand, soil parameters and vegetation structure together and on the other hand spatial, environment and soil structures together were the most important factors in defining patterns of carabid beetles. Considering also *A. altissima* vegetation structure as factor (Fig. A.1 a,b in Appendix A in Supplementary material), its presence explained carabid beetle distribution, but less than spatial and environment relative factors. Non-invaded vegetation considered as factor did not influence carabids species pattern, since most of the variations was explained by shared variation between environmental and spatial factors.

Fig. 3. Result of the variance partitioning analysis, showing the contribution of Spatial factors, Environmental variables (Env), Soil and Vegetation Structure factors (Struct) to the variation in carabid beetles (a) and plants (b).

	Beetle		**Plant**	
Soil Variables	**R^2**	p-value	**R^2**	p-value
Soil rock fragments	0.39	**0.019**	0.45	**0.010**

Soil fine earth fraction	0.28	0.065	0.35	**0.037**
Soil humidity	0.27	**0.077**	0.29	0.066
Soil bulk density	0.35	**0.033**	0.36	**0.030**
Soil porosity	0.47	**0.005**	0.48	**0.006**
Soil mean weight diameter	0.33	**0.037**	0.35	**0.036**
Environmental Variables	**R^2**	p-value	**R^2**	p-value
Latitude	0.63	**0.000**	0.52	**0.003**
Longitude	0.84	**0.001**	0.86	**0.000**
Slope	0.52	**0.005**	0.61	**0.002**
Elevation	0.44	**0.008**	0.35	**0.030**
Northness	0.14	0.303	0.14	0.308
Eastness	0.01	0.904	0.03	0.790
Doline depth	0.40	**0.022**	0.30	0.065
Karstification	0.58	**0.002**	0.64	**0.001**
Vegetation Structure	**R^2**	p-value	**R^2**	p-value
AH_mean	0.40	**0.019**	0.54	**0.005**
AD_mean	0.37	**0.026**	0.49	**0.008**
A_density	0.32	**0.047**	0.42	**0.017**
N_A	0.32	**0.047**	0.42	**0.017**
Cop_A	0.25	0.096	0.40	**0.020**
IH_mean	0.54	**0.002**	0.50	**0.003**
ID_mean	0.49	**0.005**	0.47	**0.006**
I_density	0.42	**0.017**	0.34	**0.043**
N_I	0.42	**0.017**	0.34	**0.043**
Cop_I	0.49	**0.005**	0.61	**0.001**
	R^2	p-value	**R^2**	p-value
Environmental variables with soil	0.58	**0.001**	0.43	**0.008**

Table 3. Environmental vectors estimated on Co-Ca ordination using *envfit.coca* function (999 permutations) and related squared correlation coefficient. In bold the significant values,for abbreviations see Section 2.4

Variance partitioning showed that 33% of the total explained variation for the ordination of carabid beetles assemblages was due to the independent effect of environment, whereas the pure effects of spatial variables, vegetation structure and soil parameters explained 8%, 10% and 1% of this total variation, respectively. If we analyze independently the effect of invaded vegetation structure, it explained the 18% of the total variance, whereas the non-invaded vegetation structure was not informative.

4. Discussion

In this study, we assessed cross-taxon congruence between carabid beetles and vascular plants among invaded *vs*. non-invaded stages along a successional gradient of vegetation (from grassland to woodland), estimating also the explicative power of biotic and abiotic factors on both communities. Since both plants and carabid beetles respond similarly to environmental gradient, plants can effectively be used as a surrogate taxon in the study area. Our findings are in agreement with Brunbjerg et al. (2018), who proved that plant species, considered along environmental gradients, are a useful surrogate for biodiversity in general.

In this context, we also proved that there is a differentiation in species communities along non-invaded vegetation stages, while this differentiation is not significant along the invaded vegetation stages. This suggests that both carabid beetle and plant communities are strongly influenced by *A. altissima*, which may promote a homogenization of the communities, fostering a subset of species typical of disturbed and anthropized area.

Carabid assemblages are known to be affected by microhabitat variation and biotic interactions at smaller scales (e.g. “patchiness”) (Niemelä et al., 1992; Antvogel and Bonn, 2001; Thomas et al., 2001; Brose, 2003; Barbaro et al., 2007; Schreiner and Irmler, 2009) and their communities have been directly related to different forest stages (Riley et Browne, 2011), ground vegetation and litter (Niemelä et al. 1993; Niemelä and Spence, 1994; Koivula, 2001; Rainio and Niemelä, 2003).

Even if many studies related carabid fauna to biotic and abiotic conditions (Rainio and Niemelä, 2003; Koivula, 2011) and to environmental variables such as temperature, rainfall, vegetation cover, soil moisture (Ings and Hartley, 1999; Jukes et al., 2001; Perner and Malt 2003; Kotze et al., 2011; Moraes et al., 2013; Lee and Albajes, 2016), it is still not completely clear which of these variables best correlate to their observed patterns of richness and abundance (Niemelä, 1996) and which are more informative at a certain scale and/or condition (e.g. preserved or altered environments, Moraes et al., 2013). In agreement with Ings and Hartley (1999), who reported that vegetation and soil factors influenced the prey of the carabids rather than Carabidae themselves, we found a strong effect of soil features on carabid beetle communities. The most important soil factors for both carabid beetles and plant species in our study area were the soil porosity and soil rock fragments, characterizing the typical Karst red soil. Karstic woodlands, especially in doline (both non-invaded and invaded), appeared to be linked to greater soil porosity whereas soil rock fragments characterize grasslands. Carabid beetles living in different types of grassland are directly associated with soil factors such as soil organic matter content and soil moisture (Luff et al., 1989; Gardner, 1991; Gardner et al., 1997) and there are many studies showing how carabid fauna is useful to discriminate with fine resolution habitats such as grassland (e.g. Tanabe et al., 2007). In our study, we found species related to grassland, those typical of open habitats, that were *Harpalus dimidiatus, Philorhizus crucifer confusus, Poecilus koyi goricianus.* The indicator species analysis confirmed *Poecilus koyi goricianus* as indicator species of grassland dominated by *A. altissima* (see Tab. A.3 in Appendix A). On the other hand, we found also many groups of carabid beetles belonging to woodland habitats such as *Synuchus vivalis, Harpalus atratus, Leistus rufomarginatus* which are thermotolerant and heliophilous species. Others are known to be typical species of more humid and fresh woods (*Licinus hoffmanseggii, Abax carinatus sulcatus*) or to be typical species of mesophilous karst woods (*Carabus catenulatus catenulatus, Molops ovipennis istrianus*) (Brandmayr et al., 1983, 2005).

In general, even if we found many species which are connected exclusively to grassland habitats, such as *Harpalus dimidiatus, Harpalus serripes, Ophonus azureus,* it is interesting to note that when *A. altissima* invaded grasslands, it promoted *Calathus cinctus*, a typical species of secondary ecosystems and degraded grasslands. The indicator species analysis confirms this pattern, with *C. cinctus* and *Synuchus vivalis* that are the only species strictly connected with invaded habitats. This result is particularly significant considering that *A. altissima* seems to be connected with an increase of distribution abundance also of another species, *Harpalus atratus*, a species connected to anthropic and disturbed areas (Brandmayr et al., 2005).

Furthermore, invaded habitats showed the highest carabid beetle species number. Several studies underlined that heterogeneous environments have usually higher diversity and abundance of carabid beetle species (Butterfield, 1997; Magura et al., 2003; Hartley et al., 2007; Fujita et al. 2008). Actually, when carabid fauna is compared between undisturbed and disturbed environments, the species number is often observed to increase in the latter ones (Brandmayr et al., 2005; Latty et al., 2006; Uehara-Prado et al., 2009). This can be a consequence of generalist species emigrating from open areas, following the appropriate conditions created by disturbance (Latty et al., 2006). Another possible interpretation of the higher species numbers observed could be seen in the higher soil humidity of the *Ailanthus* wood that favors the concentration of wet soil dwelles, like *Carabus granulatus*. There is a clear evidence from the literature that carabid assemblage composition

changes under structural changes of the habitat (Scott and Anderson, 2003), and that habitat type represents the most important factor explaining their distribution patterns at the regional and landscape scales (Dufrêne, 1992; Penev, 1996; Aviron et al., 2005; Eyre et al., 2005; Hartley et al., 2007).
Concerning the impact of invasive species on ecosystems, it is interesting to cite the effects of *Robinia pseudoacacia* on 18 arthropod taxa in woodlands (Buchholz et al., 2015); it emerges that the invasion of this tree can induce species turnover in ground-dwelling arthropods, but it is not connected necessarily with reducing in arthropod species abundances or diversity.
Carabid beetles living in different types of grassland are directly associated with soil factors such as soil organic matter content and soil moisture (Luff et al., 1989; Gardner, 1991; Gardner et al., 1997) and there are many studies showing how carabid fauna is useful to discriminate with fine resolution habitats such as grassland (e.g. Tanabe et al., 2007).

The highly complex of environmental, soil and vegetation structure variables which explains the cross-taxon congruence of carabid beetle and plant communities, confirms the various biotic and abiotic factors (Judas et al., 2002; Samin et al., 2011) affecting carabid beetles in their distribution, both within and between habitats (Thiele, 1977, 1979; Lövei and Sunderland, 1996). Our study area is intentionally localized, so that we did not expect to observe a great influence of environmental and, in particular, climatic parameters (Duan et al., 2016), that usually become more important in large study areas due to more pronounced gradients (Qian and Kissling, 2010; Toranza and Arim, 2010). An in-depth analysis among the environmental variables showed that plant and carabid beetle assemblages responded to almost the same variables, such as slope, elevation, karstification. Elevation is commonly considered as a whole array of environmental factors (Duan et al., 2016), and its crucial role as explanatory environmental factor for the species. The resulting congruence in cross-taxon is furthermore an evidence that elevation is strongly correlated not only with intermediate and large study areas, but also with the small ones. Karstification is another important factor (more in plant than in carabid beetle distribution) that must be taken into account: a strong relationship degree was already known for the two sphodrine species, *Laemostenus elongatus* and *Laemostenus cavicola*, that in our study area were present in relation only to doline forest plots (Brandmayr et al., 1980).

The combination of soil and vegetation structure together expressed the 10% of the total variation, and this is in accordance with the main known factors driving the distribution of carabid beetles, that are always related to micro- and mesoscale landscape (Barbaro et al., 2007), and that take into account microclimate, vegetation structure, prey density, predation, competition or localized

oviposition sites (Niemelä et al., 1992; Antvogel and Bonn, 2001; Thomaset al., 2001; Magura, 2002; Brose, 2003). However, all the environmental variables combined with soil parameters were really significant for carabid beetle's distribution. The effect of vegetation structure, in particular those of the canopy of the native species, was already reported to be an important factor conditioning carabid beetle's assemblages (Gardner, 1991; Sanderson et al., 1995; Brandmayr et al., 2005; Tanabe et al., 2007) thanks to the greater shading and water uptake caused by larger trees, which in turn affects incoming solar radiation, light availability, soil moisture, humidity and the composition of the flora (Ings and Hartley, 1999). Shady humid conditions are associated with many species of carabid beetles especially in the early stages of their development (Thiele, 1977), whereas other species are associated with more dry and open conditions. A good example of these indirect effects can be observed in the distributions of *Leistus rufomarginatus, Carabus catenulatus catenulatus, Carabus caelatus schreiberi, Molops ovipennis istrianus, Abax parallelepipedus subpunctatus, Calosoma sycophanta:* all these species were more present in the habitats of more developed, older woods, suggesting a preference for mature woodland (Lindroth, 1985). Ings and Hartley (1999) confirmed these observations and suggested that species are responding to the shady and humid microclimate found under large and old trees, rather than to the presence of mature trees *per se*. Furthermore, in contrast with Tanabe et al. (2007), it is worth nothing that the different wood habitats were grouped separately in the Co-correspondence analysis (Fig. 2).
We found different species communities: thermotolerant and heliophilous species (such as *Synuchus vivalis, Harpalus atratus, Leistus rufomarginatus*), species typical of more humid and fresh wood (*Licinus hoffmanseggii, Abax carinatus sulcatus*), species typical of mesophilous karst wood (*Carabus catenulatus catenulatus, Molops ovipennis istrianus*) (Brandmayr et al., 2005). Their habitat affinity in the Triestine Karst has been carefully described analyzing the main bioclimate gradient from deciduous woodlands to Mediterranean wood types in Brandmayr et al. (1983).

Summing up, the most important variables showing a determinant effect on congruence across taxa were the structure of non-invaded vegetation and habitat type, considering the successional gradient of vegetation from grassland to wood. On the contrary, if we consider sites dominated by *A. altissima*, in correspondence of habitat type change, the structure of invaded vegetation and carabid assemblages remain almost the same. This fact confirms the known concept that carabid beetles show a positive relationship with environmental parameters such as vegetation cover (Thiele, 1977; Gardner, 1991; Gardner et al., 1997; Sanderson et al., 1995; Ings and Hartley, 1999; Eyre et al., 2001; Brandmayr et al., 2005; Desender et al., 2013; Alignier and Aviron, 2017), despite the strength of this connection is stronger in non-invaded habitats compared to the ones invaded by *A. altissima.*

5. Conclusions

Our results suggest that spatial distribution patterns of carabid beetles in the study area were mainly determined by environmental parameters rather than vegetation or spatial structure. Interestingly, we observed that more diversified communities of carabid beetles and plants occurred in non-invaded habitats, while trivialized communities characterized invaded areas. Additionally, the typical carabid species connected with *A. altissima* stands were those mainly common in anthropized and degraded environments. Finally, plants and carabid beetles respond to environmental variables in the same way and, in particular, plants respond to the same underlying main gradient, being at least sensitive to different conditions as carabid beetles (Gioria et al., 2009). In conclusion, plants best represent the diversity of carabid beetles in NAK region and can thus be defined as a surrogate group for carabid beetles, as already found by Lários et al. (2017) for other animal groups in Neotropical regions.

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Appendix A. Supplementary data

References

Alignier, A., Aviron, A., 2017. Time-lagged response of carabid species richness and composition to past management practices and landscape context of semi-natural field margins. J Environ Manage 204, 282-290. https://doi.org/10.1016/j.jenvman.2017.08.054

Andersen, A.N., Hoffmann, B.D., Müller, W.J., Griffiths, A.D., 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. J Appl Ecol 39 (1), 8-17. https://doi.org/10.1046/j.1365-2664.2002.00704.x

Antvogel, H., Bonn, A., 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24, 470-482. https://doi.org/10.1111/j.1600-0587.2001.tb00482.x

Aviron, S., Burel, F., Baudry, J., Schermann, N., 2005. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. Agr, Ecosyst Environ 108, 205-217. https://doi.org/10.1016/j.agee.2005.02.004

Ballero, M., Ariu, A., Falagiani, P., 2003. Allergy to *Ailanthus altissima* (tree of heaven) pollen. Eur J allergy clin immunol 58 (6), 532-533. https://doi.org/10.1034/j.1398-9995.2003.00172.x

Barbaro, L., Rossi, J.P., Vetillard, F., Nezan, J., Jactel, H., 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. J biogeogr 34 (4), 652-664. https://doi.org/10.1111/j.1365-2699.2006.01656.x

Barbato, D., Perini, C., Mocali, S., Bacaro, G., Tordoni, E., Maccherini, S., ... and Salerni, E., 2019. Teamwork makes the dream work: Disentangling cross-taxon congruence across soil biota in black pine plantations. Sci Total Environ 656, 659-669. https://doi.org/10.1016/j.scitotenv.2018.11.320

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., ... and Pergl, J., 2014. A unified classification of alien species based on the magnitude of their environmental impacts. PLoS biol 12(5), e1001850. https://doi.org/10.1371/journal.pbio.1001850

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045-1055. https://doi.org/10.2307/1940179

Brandmayr, P., Colombetta, G., Drovenik, B., Forti, F., Poldini, L., Brandmayr, Z., 1980. Etude multidisciplinaire sur l'écologie de quelques Carabides endogés (Coleoptera, Carabidae). Mem. Biospéol., 7, 85-98. Moulis, France.

Brandmayr, P., Colombetta,G., Polli, S., 1983. Waldcarabiden des Triester Karstes als Indikatoren des makroklimatischen Uebergangs vom kontinentalen Europa zur Mediterraneis. Zool Jb. Syst., Jena 110, 201-220.

Brandmayr, P., Zetto, T., Pizzolotto, R., 2005. I Coleotteri Carabidi per la valutazione ambientale e la conservazione della biodiversità [Carabid Beetles for environmental assessment and biodiversity conservation. A Primer]. APAT, Manuale operativo 34/2005, Roma.

Braun-Blanquet, J., 1964. Pflanzensociologie. Grundzuge der Vegetationskunde. 3rd Edition, Springer Verlag, Berlin

Briggs, J.C., 2013. Invasion ecology: Origin and biodiversity effects. Environmental Skeptics and Critics 2 (3), 73-81.

Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135, 407-413. https://doi.org/10.1007/s00442-003-1222-7

Brunbjerg, A.K., Bruun, H.H., Dalby, L., et al., 2018. Vascular plant species richness and bioindication predict multi-taxon species richness. Methods Ecol Evol. 9: 2372–2382. https://doi.org/10.1111/2041-210X.13087

Buchholz, S., Tietze, H., Kowarik, I., Schirmel, J., 2015. Effects of a Major Tree Invader on urban woodland arthropods. PloS ONE 10 (9), e0137723. https://doi.org/10.1371/journal.pone.0137723

Butterfield, J., 1997. Carabid community sucession during a forestry cycle in conifer plantations. Ecography 20 614-625.

Castagneyrol, B., Jactel, H., 2012. Unraveling plant-animal diversity relationships: a meta-regression analysis. Ecology 93, 2115-2124.

Castro-Díez, P., Valle, G., González-Muñoz, N., Alonso, Á., 2014. Can the Life-History Strategy Explain the Success of the Exotic Trees Ailanthus altissima and Robinia pseudoacacia in Iberian Floodplain Forests? PLoS ONE 9(6), e100254. https://doi:10.1371/journal.pone.0100254

Clark, N.A., Wynne, R.H., Schmoldt, D.L., 2000. A Review of Past Research on Dendrometers. Forest Sci 46 (4), 570-576.

da Silva, P., Aguair, C.A.S., Niemelä, J., Sousa, J.P., Serrano, A.R.M., 2008. Diversity patterns of ground-beetles (Coleoptera: Carabidae) along a gradient of land-use disturbance. Agr, Ecosyst Environ 124, 270-274.

De Caceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574.

Desender, K., 1994. Carabid Beetles: Ecology and Evolution. Edited by: Academic Publishers, 87-91.

Desender, K., Dufrêne, M., Loreau, M., Luff, M.L., Maelfait, J-P., 2013. Carabid beetles: ecology and evolution. Springer Science & Business Media, pp. 476

Duan, M., Liu, Y., Yu, Z., Baudry, J., Li, L., Wang, C., Axmacher, J.C., 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. Sci rep-UK 6, 23511. http://doi: 10.1038/srep23511.

Dufrêne, M., 1992. Biogéographie et écologie des communautés de Carabidae en Wallonie. PhD Thesis, Université Catholique de Louvain, Brussels, Belgium.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Enescu, C.M., Houston Durrant, T., Caudullo, G., 2016. *Ailanthus altissima* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg.

ESRI 2014. ArcGIS Desktop: Release 10.2.1. Redlands, CA, USA: Environmental Systems Research Institute.

Eyre, M., Luff, M., Phillips, D., 2001. The ground beetles (Coleoptera: Carabidae) of exposed riverine sediments in Scotland and northern England. Biodivers Conserv 10, 403-426. https://doi.org/10.1023/A:1016618610949

Eyre, M.D., Rushton, S.P., Luff, M.L., Telfer, M.G., 2005. Investigating the relationships between the distribution of British ground beetle species (Coleoptera, Carabidae) and temperature, precipitation and altitude. J biogeogr 32, 973-983. https://doi.org/10.1111/j.1365-2699.2005.01258.x

Forti, F., 1982. Invito alla conoscenza del Carso triestino. cenni sull'origine e sulla struttura dei fenomeni carsici. andar sul carso per vedere e conoscere. Vol (2). Edizioni LINT, Trieste.

Fujita, A., Maeto, K., Kagawa, Y., Ito, N. 2008. Effects of forest fragmentation on species richness and composition of ground Beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. Entomol Sci 11, 39-48. https://doi.org/10.1111/j.1479-8298.2007.00243.x

Gardner, S.M., 1991. Ground beetle (Coleoptera: Carabidae) communities on upland heath and their association with heathland flora. J Biogeog 18, 281-289. https//doi.org/10.2307/2845398

Gardner, S.M., Hartley, S.E., Davies, A., Palmer, S.C.F., 1997. Carabid communities on heather moorlands in northeast Scotland: the consequences of grazing pressure for community diversity. Biol Conserv 81, 275-286. https://doi.org/10.1016/S0006-3207(96)00148-6
Gioria, M., Schaffers, A., Bacaro, G., Feehan, J., 2011. The conservation value of farmland ponds: predicting water beetle assemblages using vascular plants as a surrogate group. Biol Conserv 143 (5), 1125-1133. https://doi.org/10.1016/j.biocon.2010.02.007

Global Invasive Species Database, 2017. Species profile: Ailanthus altissima. https://www.iucngisd.org/gisd/species.php?sc=319 (accessed 06 December 2017).

Grigorescu, I., Dumitraşcu, M., Kucsicsa, G., Doroftei, M., Năstase, M., Dragotă, C.S., 2016. Predicting the Potential Distribution of *Ailanthus altissima*, an Invasive Terrestrial Plant Species in Măcin Mountains National Park (Romania). In: Koulov, B., Zhelezov, G. (Eds). Sustainable Mountain Regions: Challenges and Perspectives in Southeastern Europe. Springer, Cham

Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J Ecol 97, 393-403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Hartley, D.J., Koivula, M.J., Spence, J.R., Pelletier, R., Ball, G.E., 2007. Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. Ecography 30, 673-684. https://doi.org/10.1111/j.2007.0906-7590.05199.x

Hodkinson, I.D., Jackson, J.K., 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. Environ manage 35 (5), 649-666. https://doi.org/10.1007/s00267-004-0211-x

Ings, T.C., Hartley, S.E., 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. Forest Ecol Manag119, 123-136.

Jeschke, J.M., Bacher, S., Blackburn, T.M., Dick J.T., Essl, F., Evans, T., ... , Pergl, J., 2014. Defining the impact of non-native species. Conserv Biol 28 (5), 1188-1194. https://doi.org/ 10.1111/cobi.12299

Judas, M., Dornieden, K., Strothmann, U., 2002. Distribution patterns of carabid beetle species at the landscape level. J Biogeogr29 (4), 491-508.

Jukes, M.R., Peace, A.J., Ferris, R., 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. For Ecol Manag 148 (1-3), 271-286. https//doi.org/0.1016/S0378-1127(00)00530-2

Kaligarič, M., Culiberg, M., and Kramberger, B., 2006. Recent vegetation history of the North Adriatic grasslands: expansion and decay of an anthropogenic habitat. Folia geobot 41(3), 241-258. https://doi.org/10.1007/BF02904940

Koivula, M., Punttila, P., Haila, Y., Niemeki, J., 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22, 424-435.

Koivula, M., 2001. Carabid beetles (Coleoptera: Carabidae) in boreal managed forests - mesoscale ecological patterns in relation to modern forestry. PhD thesis, Helsinki, Finland: University of Helsinki.

Koivula, M., 2011. Useful model organisms, indicator, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. Zookeys 100, 287-317. https://doi.org/10.3897/zookeys.100.1533

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G.L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R., Zetto, T., 2011. Forty years of carabid beetle research in Europe-from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. ZooKeys (100), 55-148. https://doi.org/doi: 10.3897/zookeys.100.1523

Kowarik, I., Böcker, R., 1984. Zur Verbreitung, Vergesellschaftung und Einbürgerung des Götterbaumes (Ailanthus altissima [Mill.] Swingle) in Mitteleuropa. Tuexenia 4: 9-29

Kowarik, I., Saümel, I., 2007. Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. Perspec. Plant Ecol Evol Syst. 8, 207-23. https://doi.org/10.1016/j.ppees.2007.03.002

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F. and Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conserv Biol 7, 796-808. https://dx.doi.org/10.1046/j.1523-1739.1993.740796.x

Lários, M.C., da Cunha, C.N., Penha, J., Landeiro, V.L., Pinho, J. B., Aragona, M., Valerio, L.M., Strüssmann, C., Marques, M.I., Lourenço, L.S., Chupel, T.F., Fernandesh, M.I., 2017. Evidence of cross-taxon congruence in Neotropical wetlands: Importance of environmental and spatial factors. Global Ecology and Conservation 12, 108-118. https://doi.org/ 10.1016/j.gecco.2017.09.003

Latty, E.F., Werner, S.M., Mladenoff, D.J., Raffa, K.F., Sickley, T.A., 2006. Response of ground beetles (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. Forest Ecol Manag 222, 335-347. https://doi.org/ 10.1016/j.foreco.2005.10.028

Lee, M. S., Albajes, R., 2016. Monitoring carabid indicators could reveal environmental impacts of genetically modified maize. Agric For Entomol 18 (3), 238-249. https://doi.org/ 10.1111/afe.12156

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd English edn. Elsevier Science BV, Amsterdam.

Legendre, P., Legendre, L.F., 2012. Numerical ecology (Vol. 24). Elsevier.

Lindroth, C.H., 1974. On the elytral microsculpture of carabid beetles (Col. Carabidae). Insect Syst Evol 5(3), 251-264. https://doi.org/ 10.1163/187631274X00290
Lindroth, C.H., 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. Vol. 15. part 1. Fauna Entomol. Skandinavica. Leiden. Copenhagen.

Lövei, G.L., Sunderland, K.D., 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annu rev entomol 41 (1), 231-256. https://doi.org/ 10.1146/annurev.en.41.010196.001311

Luff, M.L., 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19 (4), 345-357. https://doi.org/ 10.1007/BF00348110.

Luff, M.L., Eyre, M.D., Rushton, S.P., 1989. Classification and ordination of habitats of ground beetles (Coleoptera: Carabidae) in northeast England. J Biogeog 16 121-130. https://doi.org/ 10.2307/2845086

Maccherini, S., Bacaro, G., Favilli, L., Piazzini, S., Santi, E., Marignani, M., 2009. Congruence among vascular plants and butterflies in the evaluation of grassland restoration success. Acta Oecol 35(2), 311-317. https://doi.org/ 10.1016/j.actao.2008.12.002

Magura, T., 2002. Carabids and forest edge: spatial pattern and edge effect. Forest Ecol Manag 157 (1), 23-37. https://doi.org/ 10.1016/S0378-1127(00)00654-X

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243-253. https://doi.org/10.1038/35012251

Marinoni, R.C., 2001. Os grupos tróficos em Coleoptera. Rev Bras Zool 18, 205-224.

Marinoni, R.C., Ganho, N., Monné, M., Mermudes, J.R., 2001. Hábitos alimentares em Coleoptera (Insecta). Ribeirão Preto, Holos, pp. 63

Martens, H., Naes, T., 1992. Multivariate Calibration. Wiley, Chicester, UK.

Martínez, A., Iturrondobeitia, J.C., Goldarazena, A., 2009. Effects of some ecological variables on carabid communities in native and non native forests in the Ibaizabal basin (Basque Country: Spain). Ann For Sci 66 (3), 1-14. Available online at: c INRA, EDP Sciences, 2009 www.afs-journal.org https://doi.org/10.1051/forest/2009003

McAvoy, T.J., Snyder, A.L., Johnson, N., Salom, S.M., Kok, L.T., 2012. Road survey of the invasive tree-of-heaven (Ailanthus altissima) in Virginia. Invas Plant Sci Mana 5 (4), 506-512. https://doi.org/10.1614/IPSM-D-12-00039.1

McGeoch, M., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biol Rev 73, 181-201. https://dx.doi.org/10.1017/S000632319700515XMotard, E., Muratet, A., Clair-Maczulajtys, D., Machon, N., 2011. Does the invasive species Ailanthus altissima threaten floristic diversity of temperate peri-urban forests? C R Biol 334, 872-879. https//doi.org/10.1016/j.crvi.2011.06.003

Motard, E., Dusz, S., Geslin, B., Akpa-Vinceslas, M., Hignard, C., Babiar, O., ... , Michel-Salzat, A., 2015. How invasion by Ailanthus altissima transforms soil and litter communities in a temperate forest ecosystem. Biol Invasions 17 (6), 1817-1832. https://doi.org/ 10.1007/s10530-014-0838-3

Moraes, R.M., Mendonça Jr, M. D.S., Ott, R., 2013. Carabid beetle assemblages in three environments in the Araucaria humid forest of southern Brazil. Rev Bras de Entomol 57 (1), 67-74 https://dx.doi.org/10.1590/S0085-56262013000100011

Niemelä, J.K., 1993. Mystery of the missing species: species-abundance distribution of boreal ground-beetles. Ann Zool Fenn 30, 169-172. https://dx.doi.org/10.3897%2Fzookeys.147.2102

Niemelä, J.K., Haila, E., Halme, E., Pajunen, T., Puntilla, P., 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. J biogeogr 19 173-181. https://doi.org/ 10.4039/N02-031

Niemelä, J.K., Langor, D., Spence, J.R., 1993. Effects of clear-cut harvesting on boreal groundbeetle (Coleoptera: Carabidae) in western Canada. Conserv Biol 7, 551-561. https://doi.org/10.1046/j.1523-1739.1993.07030551.x

Niemelä, J.K., Spence, J.R., 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. Ecography 17, 166-175. https://doi.org/10.1111/j.1600-0587.1994.tb00090.x

Niemelä, J.K., 1996. Invertebrates and Boreal Forest Management. Conserv Biol 11(3), 601–610

Oertli, S., Müller, A., Steiner, D., Breitenstein, A., Dorn, S., 2005. Cross-taxon congruence of species diversity and community similarity among three insect taxa in a mosaic landscape. Biol Conserv 126, 195-205. https://doi.org/10.1016/j.biocon.2005.05.014

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P, McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. Vegan: Community Ecology Package. R Package Version 2.5-2.

Pearson, L., David, Carroll, S.,. 1998. Global Patterns of Species Richness: Spatial Models for Conservation Planning Using Bioindicator and Precipitation Data. Conserv Biol 12. 809 - 821. https://doi.org/10.1111/j.1523-1739.1998.96460.x.

Penev, L., 1996. Large-scale variation in carabid assemblages, with special reference to the local fauna concept. Ann Zool Fenn 33, 49-63.

Perner, J., Malt, S., 2003. Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. Agr Ecosyst Environ. 98 (1-3), 169-181. https://doi.org/10.1016/S0167-8809(03)00079-3

Petruzzellis, F., Peng, G., Tyree, M. T., Tonet, V., Savi, T., Torboli, V., Pallavicini, A., Bacaro, G., Nardini, A. (2019a). Plasticity of functional traits of tree of heaven is higher in exotic than in native habitats. Trees, in press. https://doi.org/10.1007/s00468-018-1787-8

Petruzzellis, F., Nardini, A., Savi, T., Tonet, V., Castello, M., Bacaro, G. (2019b). Less safety for more efficiency: water relations and hydraulics of the invasive tree Ailanthus altissima (Mill.) Swingle compared with native Fraxinus ornus L. Tree Physiol 39, 76-87. https://doi.org/10.1093/treephys/tpy076

Poldini, L. 2009. Guide alla Flora – IV. La diversità vegetale del Carso fra Trieste e Gorizia. Lo stato dell'ambiente. Le guide di Dryades 5 – Serie Flore IV (F – IV). Trieste: Edizioni Goliardiche.

Pyšek, P., Richardson, D.M,, Pergl, J., Jarošík, V., Sixtova, Z., Weber, E., 2008. Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23, 237-244. https://doi.org/10.1016/j.tree.2008.02.002PMID:18367291

Qian, H., Kissling, W.D., 2010. Spatial scale and cross-taxon congruence of terrestrial vertebrate and vascular plant species richness in China. Ecology 91, 1172-1183.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria.

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers Conserv 12 (3), 487-506. https://doi.org/10.1023/A:1022412617568

Rennie, J.C., 1979. Comparison of Height-Measurement Techniques in a Dense Loblolly Pine. South J Appl For 3 (4), 146-148.

Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species-a global review. Divers Distrib 17, 788-809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Ribera, I., Doledec, S., Downie, I.S., Foster, G.N., 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82, 1112–1129.

Riley, K.N., Browne, R.A., 2011. Changes in ground beetle diversity and community composition in age structured forests (Coleoptera, Carabidae). In: Erwin, T. (Ed.), Proceedings of a symposium honoring the careers of Ross and Joyce Bell and their contributions to scientific work. Burlington, Vermont, 12-15 June 2010. ZooKeys 147: 601-621. https://doi.org/10.3897/zookeys.147.2102

Rooney, R.C., Azeria, E.T., 2014. The strength of cross-taxon congruence in species composition varies with the size of regional species pools and the intensity of human disturbance. J biogeogr 42 (3), 439-451. https://doi.org/10.1111/jbi.12400..

Rouget, M., Robertson, M. P., Wilson, J. R., Hui, C. , Essl, F. , Renteria, J. L., Richardson, D. M. and Kühn, I., 2016. Invasion debt – quantifying future biological invasions. Divers Distrib 22, 445-456. https://doi.org/10.1111/ddi.12408

Samin, N., Sakenin, H., Kesdek, M., Imani, S., 2011. Ground beetles (Coleoptera: Carabidae) from some regions of Iran. Linzer biol. Beitr. 43 (1), 873-880.

Sætersdal, M., Gjerde, I., Blom, H.H., Ihlen, P.G., Myreseth, E.W., Pommeresche, R., Skartveit, J., Solhøyb, T., Aasc, O., 2003. Vascular plant as a surrogate species group in complementary site selection for bryophytes, macro-lichens, spiders carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. Biol Conserv 115, 21-31.

Sanderson, R.A., Rushton, S.P., Cherrill, A.J., Byrne, J.P., 1995. Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. J Appl Ecol 32 (3), 506-518. https://doi.org/10.2307/2404648

Santi, E., Bacaro, G., Rocchini, D., Chiarucci, A., Bonini, I., Brunialti, G., Muggia, L., Maccherini, S., 2016. Methodological issues in exploring cross-taxon congruence across vascular plants, bryophytes and lichens. Folia Geobot 51, 297-304. https://doi.org/10.1007/s12224-016-9265-9

Sax, D.F., 2002a. Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. Global Ecol Biogeogr 11, 49–58.

Sax, D.F., 2002b. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. Divers Distrib 8, 193–210

Schaffers, A.P., Raemakers, I.P., Sýkora, K.V., ter Braak, C.J.F., 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89, 782-794.

Schirmel, J., Buchholz, S., 2013. Invasive moss alters patterns in life-history traits and functional diversity of spiders and carabids. Biol Invasions 15, 1089–1100. https://doi.org/10.1007/s10530-012-0352-4Schlaepfer, M.A., Sax, D.F., Olden, J.D., 2010. The Potential Conservation Value of Non-Native Species. Conserv Biol 25 (3), 428-437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Schreiner, R., Irmler, U., 2009. Niche differentiation and preferences of *Elaphrus cupreus* Duftschmid, 1812 and *Elaphrus uliginosus* (Fabricius, 1792) (Coleoptera: Carabidae) as reason for their different endangerment in Central Europe. J Insect Conserv 13, 193-202. https://doi.org/10.1007/s10841-008-9142-9

Scott, W.A., Anderson, R., 2003. Temporal and spatial variation in carabid assemblages from the United Kindom Environmental Change Network. Biol Conserv 110, 197–210

Simpson, G.L., 2009. Co-correspondence analysis ordination methods. (R package version 0.3-0).

Sladonja, B., Sušek, M., Guillermic, J., 2015. Review on invasive tree of heaven (Ailanthus altissima (Mill.) Swingle) conflicting values: assessment of its ecosystem services and potential biological threat. Environ Manage 56:1009–1034. https://doi.org/10.1007/s00267-015-0546-5

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: Community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conserv Biol 18, 167-173.

Tanabe, S-I., Kholin, S.K., Cho, Y-B., Hiramatsu, S-I., Ohwaki A., Koji, S., Higuchi, A., Storozhenko, S.Y., Nishihara, S., Esaki, K., Kimura, K., Nakamura, K., 2007. A Higher-Taxon Approach With Soil Invertebrates To Assessing Habitat Diversity In: Nakagoshi, N., Fu, B.J., Morimoto, Y. (Eds.), East Asian Rural Landscapes. Chapter eleven, Landscape Ecological Applications in Man-Influenced Areas: Linking Man and Nature Systems. Springer 163-177.

Taylor, R.J., Dorann, N., 2001. Use of invertebrates as indicators of the ecological sustainability of management under the Montreal process. J Insect Conserv 5, 221-231.

ter Braak, C.J.F., Schaffers, A.P., 2004. Co-correspondence analysis: a new ordination method to relate two community compositions. Ecology, 834-846.

Thiele, H.U., 1977. Carabid Beetles in Their Environments: A Study on Habitat Selection by Adaptations in Physiology and Behaviour. Springer, Berlin.

Thiele, H.U., 1979. Relationships between annual and daily rhythms, climatic demands and habitat selection in carabid beetles. In: Erwint, T.L., Ball, G.E., Whitehead, D.R.(Eds.), Carabid beetles: Their evolution, natural history, and classification. W. Junk, The Hague.

Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Garcia, A.F., Marshall, E.J.P., 2001. Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. J Appl Ecol 38, 100-116.

Toranza, C., Arim, M., 2010. Cross-taxon congruence and environmental conditions. BMC Ecol 10, 1-9.https://doi.org/10.1186/1472-6785-10-18

Tordoni, E., Napolitano, R., Maccherini, S., Da Re, D., Bacaro, G., 2018. Ecological drivers of plant diversity patterns in remnants coastal sand dune ecosystems along the northern Adriatic coastline. Ecol Res 1-12. https://dx.doi.org/10.1007%2Fs11284-018-1629-6

Tsao, R., Romanchuk, F.E., Peterson, C.J., Coats, J.R., 2002. Plant growth regulatory effect and insecticidal activity of the extracts of the Tree of Heaven (*Ailanthus altissima* L.). BMC Ecol 2, (1): 1. https://dx.doi.org/10.1186%2F1472-6785-2-1

Uehara-Prado, M., Fernandes, J.O., Bello, A.M., Machado, G., Santos, A.J., Vaz-de-Mello, F.Z., Freitas, A.V.L., 2009. Selecting terrestrial arthropods of indicators of small-scale disturbance: A first approach in the Brazilian Atlantic Forest. Biol Conserv 142, 1220- 1228. https://doi.org/10.1016/j.biocon.2009.01.008

Vila, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Médail, F., Moragues, E., Traveset, A., Troumbis, A.Y., Hulme, P.E., 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J biogeogr 33, 853-861.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, ..., Pyšek P, 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol lett 14, 702-708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Villa-Castillo, J., Wagner, M.R., 2002. Ground beetle (Coleoptera: Carabidae) species assemblages as an indicator of forest condition in northern Arizona ponderosa pine forests. Environ Entomol 31 (2), 242-252. https://doi.org/10.1603/0046-225X-31.2.242Westgate, M.J., Barton, P.S., Lane, P.W., Lindenmayer, D.B., 2014. Global meta-analysis reveals low consistency of biodiversity congruence relationships. Nature Commun 5, 3899. https://doi.org/10.1038/ncomms4899

Wilson, E.O., 1987. The little things that run the world (the importance and conservation of invertebrates). Conserv Biol 1, 344-346. https://doi.org/10.1111/j.1523-1739.1987.tb00055.x

Wilson, J.R.U., García-Díaz, P., Cassey, P., Richardson, D.M., Pyšek, P., Blackburn, T.M., 2016. Biological invasions and natural colonisations are different - the need for invasion science. NeoBiota 31, 87-98. https://doi.org/10.3897/neobiota.31.9185

Zhang, X., Zhao, G., Zhang, X., Li, X., Yu, Z., Liu, Y., Liang, H., 2017. Ground Beetle (Coleoptera: Carabidae) Diversity and Body-Size Variation in Four Land Use Types in a Mountainous Area Near Beijing, China. The Coleopterists Bulletin 71 (2), 402-412. https://doi.org/10.1649/0010-065X-71.2.402