Cross-taxon congruence between predatory arthropods and plants across Mediterranean agricultural landscapes

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ABSTRACT

Although arthropods are among the most diverse, abundant and ecologically important animals in terrestrial ecosystems, they are generally neglected in most biodiversity inventories due to their complex systematics and overwhelming diversity, coupled with the current decline in the number of taxonomists. For this reason, several surrogate groups for arthropod diversity have been proposed, with plants being identified as a good putative cross-taxon indicator. By sampling plants and three groups of ground-dwelling arthropods (rove beetles, ground beetles and spiders) in 300 sites across 15 landscapes including multiple semi-natural and agricultural habitats, we tested for habitat-dependence and scale-dependence in the cross-taxon congruence. Plant species richness was a poor predictor of the species richness of predatory arthropods. Among the predator groups, ground beetles appeared as the best potential surrogate for the other ground-dwelling predators. This is backed by the fact that ground beetles were extremely diverse and abundant in all habitats and are usually easier to identify than both rove beetles and spiders. Decreasing the scale at which the cross-taxon congruence was tested improved the strength of the cross-taxon congruence. Although plant species richness was not a suitable indicator for the diversity of predatory arthropods, vegetation structure played a significant role in influencing cross-taxon congruence in both natural and agricultural habitats. Our results highlight the need to explore the cross-taxon relationships at a fine habitat resolution scale, as strong correlations were obtained only by taking into account habitat identity.

1. Introduction

Arthropods are the most diverse, abundant and ecologically important animals in terrestrial ecosystems (Kremen et al., 1993), in both natural and managed habitats (Birkhofer et al., 2018). They are also particularly threatened by multiple human impacts, including the conversion of natural habitats into agricultural fields (Gámez-Virués et al., 2015), and a general decline in arthropod diversity and abundance has been recently reported (Hallmann et al., 2017; Seibold et al., 2019). Yet, arthropods are generally neglected in most biodiversity inventories due to their complex systematics and high diversity coupled with current negative trends in the number of taxonomists (Heink and Kowarik, 2010; Lovell et al., 2007; Navarro et al., 2017; Noss, 1990). In the last

decades, an increasing number of studies have highlighted the need for the identification of a small number of surrogates that can act as indicators of the overall biodiversity of an area (Birkhofer et al., 2018; Harry et al., 2019; Larrieu et al., 2018; Oberprieler et al., 2020). The fundamental requisite of a good surrogate taxon is for its diversity to covary with that of other groups (Oberprieler et al., 2019; Westgate et al., 2017).

Plants have often been proposed as diversity indicators for many arthropod groups (Bucher et al., 2019; Larrieu et al., 2018; Uboni et al., 2019; Vasconcelos et al., 2019). This is true not only for herbivorous arthropods, but also for predators. Predatory arthropods depend on herbivore communities to thrive, which in turn depend on plant assemblages (Ebeling et al., 2018). Additionally, many generalist

predatory arthropods have a direct trophic link with plants, as they supplement their diet with plant-based food (Escalona et al., 2017; Lami et al., 2020). Finally, predators can also use plants as refuge (Nell and Mooney, 2019). However, an increasing body of research suggests that plants may not always be an effective surrogate taxon (Dorey et al., 2018; Sabatini et al., 2016; Westgate et al., 2017), especially for arthropods (Schalkwyk et al., 2019). Correlations between plants and arthropods were found to be stronger for herbivores and plant-associated species (Bucher et al., 2019; Vasconcelos et al., 2019), while little is known on the suitability of plants to predict diversity of predator taxa that depend on other resources. However, predatory arthropods are important component of both agricultural and natural habitats (Landis et al., 2000; Thorbek and Bilde, 2004) and indicator taxa for their diversity are urgently needed. An alternative approach would be to use one predator group as a surrogate taxon for the diversity of other predators, as the similar ecological niche would imply a relatively high chance to respond similarly to environmental factors. In spite of the aforementioned difficulties in arthropod taxonomy, there are indeed some groups that are relatively well known and easy to identify, which would make them potentially good candidates for the role of surrogate taxa – a typical example being represented by ground beetles (Coleoptera: Carabidae) (Johan Kotze et al., 2011).

Even if different taxa have been shown to exhibit varying distribution patterns across spatial scales and habitats (Bucher et al., 2019; Burrascano et al., 2018; Oberprieler et al., 2019), most of the studies aimed at identifying surrogates for conservation planning have been carried out at coarse spatial scales (Lovell et al., 2007). As cross-taxon congruence is expected to vary among habitats (Bacaro et al., 2019; Larrieu et al., 2019), contrasting results may emerge when switching the scale from regional to local (i.e. habitat level). Semi-natural habitats are generally expected to host a higher diversity of arthropods (especially when compared to agro-ecosystems) and thus to be of higher value for conservation and ecosystem services' provision. However, as agricultural fields are progressively occupying larger areas on Earth (Foley, 2005), their management is becoming critical in supporting the diversity and abundance of arthropod predators, which in turn may help to ensure adequate biocontrol services in these areas (Landis et al., 2000). For this reason, finding the correct level of resolution (at the regional, local or habitat scale) and discriminating between semi-natural and agricultural habitats is crucial for the identification of effective surrogate taxa, which in turn can inform conservation strategies by acting as easy-to-survey indicators of the state of biodiversity in a given moment and place.

The aim of this study was to explore the distribution of ground-dwelling arthropod predators and vascular plants in 300 sites across 15 landscapes encompassing four types of agricultural and semi-natural habitats. Selected arthropod taxa were rove beetles (Coleoptera: Staphylinidae), ground beetles, and ground-dwelling spiders (Araneae). These important and ecologically diverse groups include mostly generalist predators which can consume a wide range of prey, with only a small percentage of omnivorous species (Birkhofer et al., 2018; Luff and Rushton, 1989; Thorbek and Bilde, 2004). However, if and how these predatory taxa are associated with each other or with plants in terms of diversity and assemblage composition is still unknown. We tested for cross-taxon congruence in both species richness and community composition (turnover) of the three predator groups and plants and explored how patterns changed among habitat types and across scales, thus assessing the role of these groups as surrogate taxa.

2. Materials and methods

2.1. Study area and site selection

Fieldwork was conducted in 2017 in the Friuli region, in north-eastern Italy. The area is an agricultural lowland region with temperate climate. The mean annual precipitation is c. 1300 mm and the mean annual temperature is *c.* 13 °C. The area is dominated by crops (both annual and perennial cultures), interspersed with small semi-natural elements. We selected 15 landscapes, each consisting of a circular area of 1 km in radius, and 20 sampling sites within each landscape, for a total of 300 sampling sites (Fig. S1). Distance among landscapes ranged from 1.89 km to 43.03 km, with a mean of 23.22 km. Site selection reflected the relative abundance of the main habitat types in each landscape and allowed to evaluate species occurrence across all the major habitats occurring across the landscape mosaic (Marini et al., 2019). In a preliminary field survey, the type of agricultural (i.e. annual or perennial crop) or semi-natural (i.e. meadow or forest) habitat was defined. Agricultural habitats were additionally classified by their specific crop type: maize, other cereals (barley and wheat), mass-flowering crops (sunflower, soy, peas, rapeseed, and *Phacelia*), vineyards and wood plantations (orchards, poplar stands and olive groves) (Table S1). In terms of agricultural treatments, the chosen crop fields were homogeneous, as no chemical treatments were applied to crops in the chosen period in the study area, and all the selected annual crops were conventionally tilled.

2.2. Data survey: ground-dwelling arthropod predators and plants

In each site, we sampled the ground-dwelling arthropod fauna of predators (Coleoptera: Staphylinidae and Carabidae; Araneae) by using pitfall traps. Traps consisted in 0.5 l plastic cups (Ø 10 cm, 14 cm depth) buried flush with the ground surface and protected from rain by plastic covers. Traps were activated with ≃ 150 ml of 40% ethylene glycol and left in the field for 28 consecutive days (May-June 2017). They were emptied and immediately reactivated after the first 14 days to avoid overfilling, resulting in 2 consecutive rounds. Because a few traps were active for only one sampling round (having been destroyed during the other), a mean abundance per species per trap was calculated for the arthropod taxa. In eight of the 300 sites, the traps were destroyed in the field in both rounds, resulting in the exclusion of those sites from the arthropod dataset. Collected specimens were stored in 70% ethanol, and then identified to the species level by morphological traits.

In each site, all vascular plants occurring in a square of 100 m^2 (10 × 10 m) were recorded. In eleven of the 300 sites, plant surveys could not be carried out due to major habitat-altering events (i.e. meadow mowing or cutting of poplar stands).

2.3. Analyses

Species rarefaction curves were constructed to describe the species accumulation in relation to sampling effort (i.e. sampled sites) for each of the four studied taxa. Abundance-based estimates were calculated using the "specaccum" function in the BiodiversityR package (Kindt and Coe, 2005) in R (R Core Team, 2016).

2.3.1. Diversity patterns

Linear mixed-effect models were used to explore how species richness, abundance and evenness of the three predator taxa varied among habitat types. Response variables were the cumulative number of species, mean abundance per species (between first and second round of sampling) and the evenness for each sampling site, whereas the habitat type was used as fixed effect. Evenness was measured using the Smith and Wilson's index (Smith and Wilson, 1996). The response variables were log-transformed to improve the linearity. For vascular plants we performed the analysis using species richness alone as response variable, as we only have occurrence data (presence/absence) for this taxon. The landscape ID was used as random factor in all models to account for spatial dependence in the design.

2.3.2. Cross-taxon congruence in species richness and community turnover

For each pair of taxa, we calculated correlations for total species richness (Pearson's correlations) and community composition turnover (Mantel's correlations). Correlations were calculated at three level of

resolution: 1) regional, with all sites pooled together (n = 281), 2) separately for habitat type (annual crop = 124; perennial crop = 56; meadow = 30; forest = 83), and 3) in the case of agricultural habitats, divided by their specific crop type: maize (n = 70), cereals (n = 26), mass-flowering crops (n = 20), vineyard (n = 34) and wood plantations (n = 20). In order to perform the Mantel test, we restricted the analysis to all sites where at least one species for each of the four taxa was collected (n = 239) and used only presence/absence data for both predators and plants. We first calculated for each taxon a distance matrix using the turnover component (i.e. replacement in species composition) of the Jaccard dissimilarity index (Carvalho et al., 2013). Distance matrices were calculated using the "betadiver" function in the "vegan" package (Oksanen et al., 2019). Dissimilarity matrices were tested the pairwise for significant correlations using 999 randomized permutations and the "mante.rtest" function in the "ade4" package. All analyses were performed in R (R Core Team, 2016).

3. Results

We collected and identified to species level 3,338 rove beetles (168 species), 30,572 ground beetles (104 species) and 7,002 spiders (94 species across 15 families), for a total of 40,912 ground dwelling predators. The most abundant species in the three groups were *Aleochara haemoptera* Kraatz, *Pterostichus melas* (Creutzer) and *Trochosa hispanica* Simon, constituting the 25%, 37% and 19% of the rove beetle, ground beetle and spider communities, respectively. Also, 459 plant species were identified, with an average 18 species per site (min = 2; max = 48). The three most abundant plant species were *Sorghum halepense* (L.), *Taraxacum* sect. and *Cynodon dactylon* (L.), present in 118, 94 and 90 of the 289 sites, respectively.

The estimated rarefaction curves for each predator taxon indicated that we collected the vast majority of species present in the area, in particular for ground beetles and spiders (**Fig. S2a**). The species rarefaction curve for plants remained steeper (**Fig. S2b**), probably because of the high number of plant species present in different habitats, particularly in meadows and perennial crops (Fig. 1).

Species richness, mean abundance and evenness of rove beetles and spiders varied in the different habitats (Fig. 2; **Table S2**), with meadows being particularly species- and individual-rich and annual crops showing the opposite trend. Species richness, abundance and evenness
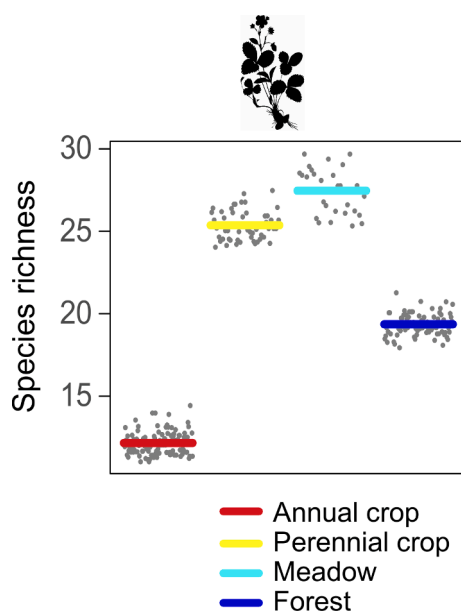

Fig. 1. Plant species richness in the four main habitat types. The plant silhouette image was downloaded from PhyloPic website.

of ground beetles did not change among habitats.

3.1. Cross-taxon congruence: General patterns

At the regional level, in terms of species richness, we detected an overall positive correlation between predator groups, whereas the correlation between predators and plants varied among taxa: correlation was positive for spiders, negative for ground beetles and non-significant for rove beetles (Fig. 3a). For community turnover, pairwise correlations were generally weaker and more variable than for species richness, without marked differences between taxa. Mantel's correlation between groups indicated that, at the regional level, changes in ground beetle species composition among sites (i.e. species turnover) were associated with changes in the communities of rove beetles, spiders and plants, whereas the other taxa (rove beetles, spiders and plants) did not show significant co-variation in species turnover (Fig. 3a).

3.2. Cross-taxon congruence at the habitat level (semi-natural and agricultural habitats)

At the habitat level, pairwise correlations in species richness between taxa of predators were quite consistent among semi-natural and agricultural habitats, whereas the negative correlation between the species richness of the two beetle groups and plants was significant only in meadows (Fig. 3b). Regarding correlations in community turnover, again the pairwise correlations between taxa of predators were weaker and more variable than for species richness. Ground beetles showed a significant correlation with plants in all habitats, while the congruence between plant species turnover and the other two predatory groups varied between habitat types. For rove beetles, it appears that the correlation trend with plants was particularly strong in meadows and annual crops, whereas for spiders, Mantel's correlation with plants was only significant in forests (Fig. 3b).

3.3. Cross-taxon congruence within crop type in agro-ecosystems

When observing the cross-taxon congruence in each crop type within the agricultural habitats, we found that the same correlation patterns in species richness recorded at the regional and habitat level was preserved for the predator taxa. In contrast, no correlation was found between species richness of predators and plants, with the exception of a negative relationship between species richness of spiders and the number of plant species in wood plantations (Fig. 3c). Regarding community turnover, ground beetles once again showed a significant correlation with plants in all crop types, while the congruence between plant species turnover and the other two groups varied among crops. Rove beetles showed a significant correlation only in maize, whereas for spiders there were significant correlations in wood plantations, maize and other cereals (Fig. 3c).

4. Discussion

Consistently with previous studies (Burrascano et al., 2018; Filgueiras et al., 2019; Harry et al., 2019; Larrieu et al., 2018; Lovell et al., 2007; Oberprieler et al., 2020; Schalkwyk et al., 2019), we found that cross-taxon congruence was generally low in terms of both species richness and community turnover, suggesting that the selected taxa are poorly representative of each other. However, increasing the level of resolution (i.e. from the regional to the habitat level) led to stronger pairwise correlations, highlighting a habitat-dependence in the cross-taxon congruence between predatory arthropods and plants. The patterns were consistent among regional, habitat and crop type scales for species richness, while for community turnover they varied from the regional to the habitat level and, in the context of agricultural habitats, among crop types.

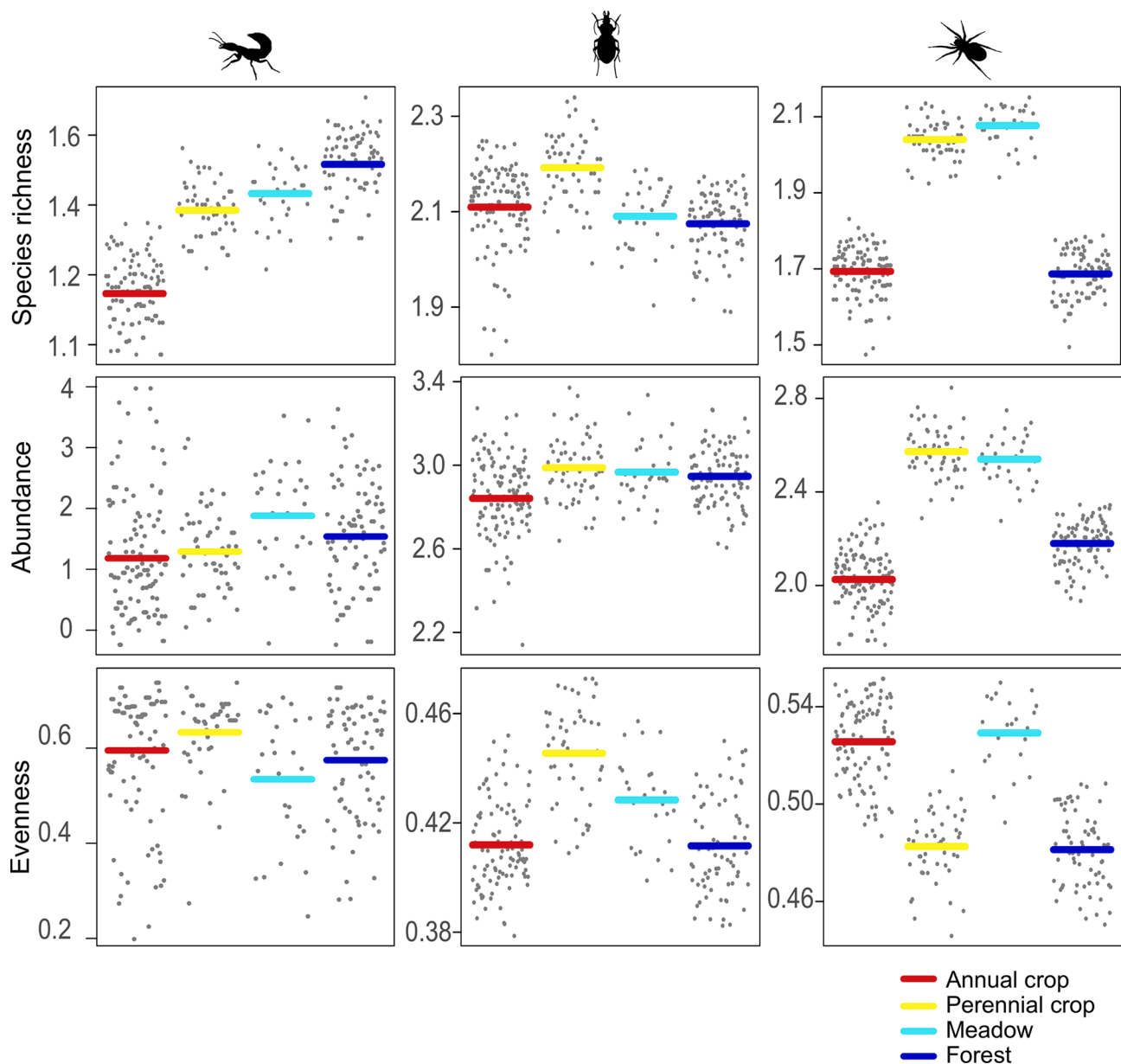Despite the general agreement that plants are usually a good

Fig. 2. Species richness, mean abundance and evenness of the three predator taxa in the four habitat types. Arthropod silhouette images were downloaded from PhyloPic website.

ecological indicator for other groups, our study points to ground beetles as the best potential surrogate group for other ground-dwelling predators. This taxon (mostly comprising generalist species) was extremely diverse and abundant in all habitats, including arable crops. Not only they tend to co-vary with other taxa but they are also taxonomically well known, and usually easier to identify than both rove beetles and spiders (Johan Kotze et al., 2011). Ground beetles are considered important biocontrol agents for both animal pests and weeds (Honek et al., 2003; Lövei and Sunderland, 1996), as well as potentially useful environmental bioindicators (Rainio and Niemelä, 2003), and as such there is great interest in their conservation, and a relatively high number of experts is available for their identification. Our results suggest that, in a variety of habitat types (both natural and agricultural), ground beetle community turnover and especially species richness would provide some indirect information about other beneficial ground-dwelling predator communities.

4.1. General patterns of cross-taxon congruence

We found that the diversity of predators co-varied, with correlations in species richness being stronger than those in community composition. It is likely that the three predator groups are influenced in a similar way by the same factors. The diversity of plants, however, is probably not among these factors, as the cross-taxon congruence between predators and plants was generally weak and not consistent among species richness and turnover metrics. In fact, in contrast with previous studies that found that plants co-varied with arthropods (Bucher et al., 2019; Larrieu et al., 2018; Uboni et al., 2019; Vasconcelos et al., 2019), our research suggests that plants were not a good surrogate taxon for predatory taxa diversity. Positive correlations between plants and arthropods have been recorded mostly for herbivorous taxa, such as lepidopterans and leafhoppers (Bucher et al., 2019). However, ground-dwelling predators that do not directly rely on plants for feeding and nesting show very different patterns. Here, we found that ground beetles were negatively associated with the species richness of plants and positively with turnover in plant
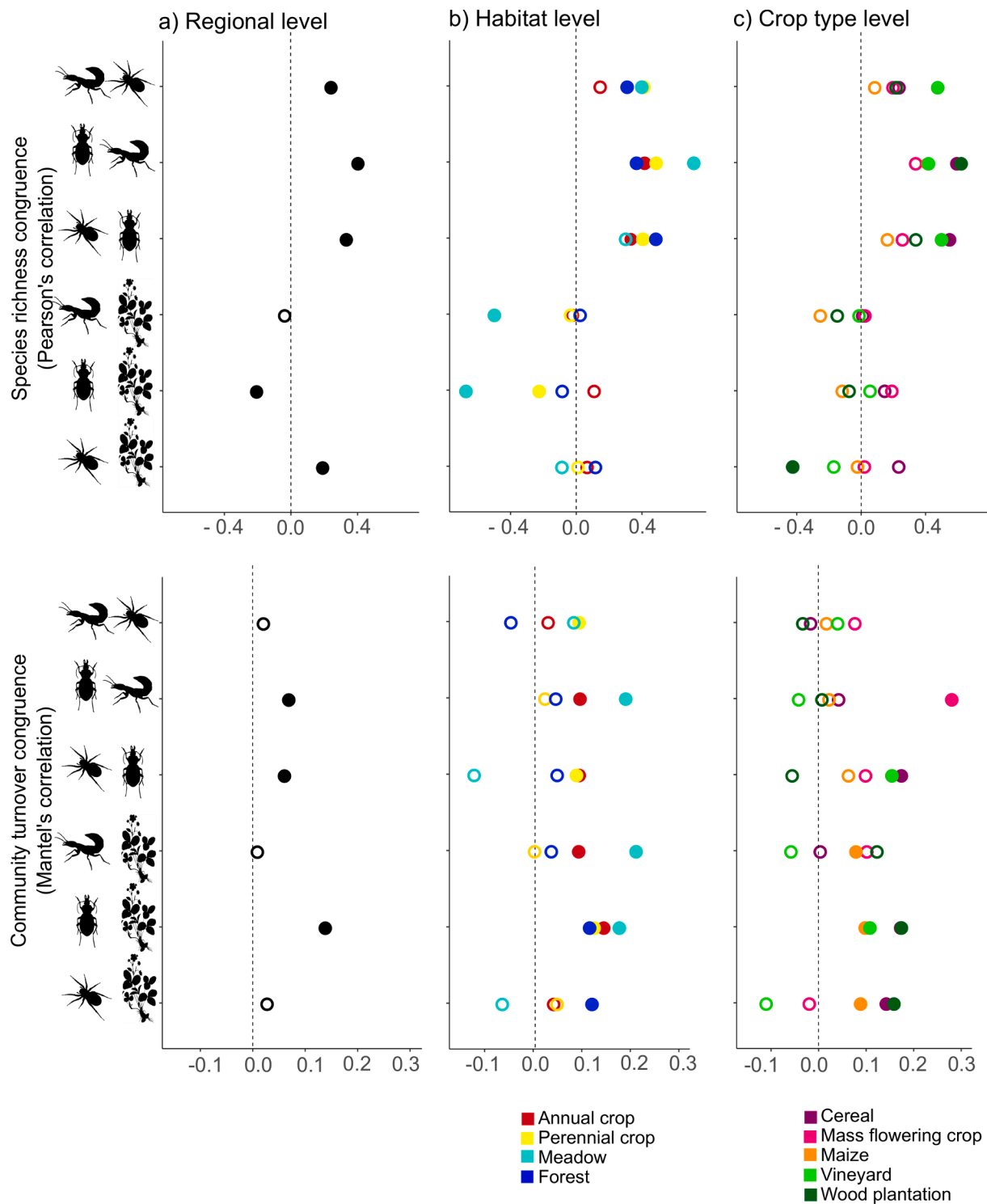
Fig. 3. Pairwise cross-taxon congruence in species richness (Pearson's correlation coefficients) and community turnover (Mantel's correlation coefficients) of the four taxa at the three scales; a) regional (all sites pooled together), b) habitat, and c) crop type. Empty dots indicate non-significant effects (p-value > 0.10). Plant and arthropod silhouette images were downloaded from PhyloPic website.

assemblages. Contrasting responses in species richness and composition were observed before (Burrascano et al., 2018; Larrieu et al., 2019), highlighting the need for considering multiple diversity metrics in cross-taxon congruence studies. While ground beetles may not be as directly reliant on plants as herbivorous taxa, they may still be influenced by vegetation structure (especially at the ground level) and the associate microclimate. These factors probably depend much more on plant community composition (and especially the identity of the most

common plant species) than on mere plant species richness. Our results seem to confirm this hypothesis.

4.2. Patterns of cross-taxon congruence in semi-natural habitats

Semi-natural habitats are pivotal for the conservation of predatory arthropods, as they provide essential resources such as food, refuges and breeding sites (Geiger et al., 2009; Landis et al., 2000). As they are often

interspersed within crops, semi-natural habitats can contribute to maintain an adequate level of diversity and ensure the provision of ecosystem services even in cropland-dominated landscapes (Holland et al., 2017). Here we found that, in forest, the species richness of all three predator taxa co-varied, whereas for species turnover only ground beetle and spider assemblages co-varied with plants. Ground beetles depends on soil characteristics while ground-dwelling spiders are primarily influenced by vegetation structure (Luff and Rushton, 1989), and both groups are linked with open habitats (Geiger et al., 2009; Harvey et al., 2008; Nardi et al., 2019). Shifts in plant community composition in forest can easily lead to shifts in habitat and soil structure causing significant changes in their assemblages and consequently explaining the co-variation between the two predator groups. This process is probably true also for rove beetles, even if the observed trend was non-significant.

Similarly, we observed a co-variation in the species richness and turnover of rove and ground beetles in meadows. In this habitat, the two groups of ground dwelling arthropods were also associated with plant species richness (negatively) and turnover (positively). It is known that carnivorous ground beetles prefer open vegetation at the ground level (Geiger et al., 2009; Harvey et al., 2008). Additionally, the low plant species richness in heavily grazed grasslands may coincide with a high diversity of ground-dwelling predators, at least for ground beetles (Harry et al., 2019). As for the forests, the dependence of both rove and ground beetles on plant turnover in meadows would at least partially explain the co-variation between the two predator groups.

4.3. Patterns of cross-taxon congruence in agro-ecosystems

While semi-natural habitats are generally highly diverse in terms of plant species, agricultural fields are almost entirely composed by a single dominant species (the crop) and usually experience higher and more frequent disturbance in the form of management practices. For these reason, agricultural fields are generally considered unfavorable habitats for predatory arthropods, with perennial crops being usually more suitable for biological control agents than the more frequently disturbed annual crops (Landis et al., 2000). Contrary to our expectations, when we explored how the cross-taxon relationships changed among agricultural habitats, we did not find strong differences between annual and perennial crops, and in both habitat types we discovered significant correlations between all predator groups and between beetles and plants. However, the situation changed by increasing the level of resolution: when we considered the specific crop type within each agricultural habitat, it became evident that cross-taxon patterns varied depending on the crop. This is coherent with the well-known fact that crop species can strongly affect how ground-dwelling predators perceive the environment (Harvey et al., 2008; Landis et al., 2000). Once again, ground beetles were the group which showed the highest number of correlations with both other predators and plants.

Spider assemblages showed no significant correlations with plants in both annual and perennial crops at the habitat level, but they co-varied with the plant community in woody plantations, maize fields and other cereal crops when considering the crop type level. This might depend on different levels of weed infestation, which in turn might be at least partially influenced by crop type and management practices. Spiders were indeed found to benefit from increasing plant diversity within crop fields (Bucher et al., 2019). Spiders, however, are also more vulnerable to crop management than rove and ground beetles (Thorbek and Bilde, 2004). There is thus also the possibility that the co-variation of spiders and plants in specific crop types might depend on both taxa being influenced by the same management practices, without plants directly influencing spider communities.

4.4. Implications for future research

In order to be considered a good surrogate, an ecological group

should show strong correlations with other taxa (e.g. coefficients $r > 0.7$) (Harry et al., 2019; Heino, 2010; Lovell et al., 2007). Similarly to previous studies (Heino, 2010; but see Sauberer et al., 2004), we found that this threshold was seldom reached (only once in our case), and that all other cases in which correlation was above 0.5 were found at the finest resolution. These results imply that, while plant richness might not be a suitable indicator for predatory arthropod diversity, vegetation structure can actually play a significant role in modifying cross-taxon congruence within both natural and agricultural habitats. The successful employment of surrogate taxa thus needs to take into account the habitat context (either macro-habitat or specific crop type), and to couple it with taxon-specific ecological needs, as the different groups showed varying degrees of congruence in the different macro-habitat types in both semi-natural and agricultural habitats. The exact role played by each habitat type in the relationships between different taxa as well as its potential variability across different geographical areas therefore should become a topic of prime importance for future investigations on the subject of surrogate taxa. Such investigations will also need to consider multiple diversity indices given that, as previously stated, different indices can yield different results. Taking into account the role of habitat context in multiple geographical areas might indeed also contribute to highlight which diversity metrics are consistently more useful in each habitat type.

CRediT authorship contribution statement

Daria Corcos: Methodology, Formal analysis, Visualization, Writing - original draft. **Francesco Lami:** Methodology, Investigation, Data curation, Writing - original draft. **Davide Nardi:** Investigation, Data curation. **Francesco Boscutti:** Investigation, Data curation. **Maurizia Sigura:** Supervision, Funding acquisition. **Filippo Giannone:** Investigation, Data curation. **Paolo Pantini:** Investigation, Data curation. **Andrea Tagliapietra:** Investigation, Data curation. **Francesco Busato:** Investigation, Data curation. **Rossella Sibella:** Investigation, Data curation. **Lorenzo Marini:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107366.

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