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Nestedness-patterns of Odonata assemblages in artificial and natural aquatic habitats reveal the potential role of drinking troughs for aquatic insect conservation

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Abstract

Nestedness patterns including both artificial and natural habitat may represent evidence of such habitats' importance in community assembly and conservation of animals inhabiting those sites. Odonata often colonize drinking troughs (artificial water reservoirs) and thus they are good study models as umbrella species. We investigated if a network of artificial (troughs) and natural (pools) aquatic habitats could create a nested subset pattern for Odonata assemblages. We surveyed all the troughs present in the Castelporziano Estate (Italy, Lazio). Odonata larvae have been collected and identified. Data of a previous paper on 18 natural pools and ponds, and our samplings of 16 troughs were organized into a presence-absence matrix. The Odonata assemblage within natural and artificial habitats is significantly nested with both NODF and T metrics. Odonata species found in the troughs represented 40% of the total species pool. Some troughs interspersed with the natural pools in the nested order: eight troughs were richer in species than some natural pools, despite the big difference in surface area. Pristine water bodies and their area may not represent major constraints for species to oviposit and for larvae to grow. Drinking troughs can be highly relevant for representing refuges in the absence or decline of natural ponds and pools: lacking in top-predators (fishes), they are small "island" habitats that support the generations of Odonata (or other aquatic macroinvertebrates) during dry periods of natural water bodies. The use and focused management of such habitats can be an effective practice for freshwater ecosystems management and Odonata conservation.

Keywords Nestedness · Odonata · Insect conservation · Artificial habitats · Drinking troughs

Introduction

Artificial water reservoirs are known to be colonized by various aquatic vertebrate and invertebrate taxa. Manmade farm and garden ponds, drinking troughs for cattle and tanks for water reservoir were found to be very important systems in: (i) increasing regional biodiversity in urban environment (Gaston et al. 2005), (ii) establishing and maintaining aquatic insect biodiversity in agricultural landscape lacking natural wetlands (Ruggiero et al. 2008), (iii) representing refuges for amphibians in the absence or decline of natural ponds (Garcia-Gonzalez and Garcia-Vazquez 2011; Buono et al. 2019). However, knowledge is lacking as regards the role of manmade waterbodies where both artificial and natural aquatic habitats are available. Since it is widely accepted that in aquatic ecosystems increasing human activity is highly related to the current biodiversity loss, an exhaustive comprehension on how aquatic systems comprising both natural and manmade habitats support local biodiversity and shape ecological processes of animal taxa is an important challenge in conservation biology and ecosystem management. Indeed, large-scale wetland loss in recent years has led to the endangered status of many aquatic species in in north-western European countries (Brinson and Malvarez 2002; Cayrou et al. 2005).

Among the animal taxa inhabiting standing waters, Odonata represent a good model organism for testing the suitability and conservation value of artificial aquatic

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habitats because (i) they are often found in various types of man-made water reservoirs, (ii) they are easily taxonomically identifiable at both larval and adult stages, (iii) we have a good knowledge of their ecology (Corbet 2004), (iv) their potential role of umbrella species for other pond invertebrates is well studied (Briers and Biggs 2003; Bried and Samways 2015). Moreover, Odonata can be used for evaluating biodiversity in secondary or man-made aquatic habitats (Bried and Samways 2015).

Odonata habitat choice depends primarily on water body area, and secondarily on habitat features (aquatic vegetation, perching sites availability, etc.) (Corbet 2004). A comprehensive view on the species–area relationship, incorporating species composition, derives from the nestedness theory: namely, an assemblage is defined as nested when species present at species-poor sites constitute a subset of the species from richer sites (Patterson and Atmar 1986). This pattern is often correlated with the variation of environmental variables among the habitat sites and the different tolerance and ecological traits of the species. Schouten et al. (2007) highlighted the strong need to study insect taxa in this framework as they represent the largest part of known biodiversity, comprise many endangered species and are highly responsive to ecosystem functions changes. Indeed, nestedness patterns in animal communities have been often found to be generated in naturally or anthropogenically fragmented landscapes (Yiming et al. 1998; Fischer and Lindenmayer 2005). Moreover, several studies applied the nestedness framework to Odonata with crucial matters of environmental conservation like monitoring of species reacting to degradation of wetlands (Sahlén and Ekestubbe 2001; Craig et al. 2008), and prediction of the trajectory of species recovery in study of restoration of seminatural habitats (Kadoya et al. 2008). Therefore, we expect that assemblage structure in standing waters networks, that are intrinsically fragmented, should proceed in a nested fashion (Cutler 1994). However, rural landscapes with small artificial aquatic habitats interspersed among natural sites provide an ecological scenario where the colonization processes by aquatic organisms can be hard to predict. The mixture of man-made and pristine aquatic habitats represents a highly diversified pool of water bodies in terms of their size, structure, hydroperiod, and biotope (Hrivnák et al. 2014).

Therefore, the aims of this study are (i) to ascertain if a network of artificial (drinking troughs) and natural (pools) aquatic habitats could generate a nested pattern for Odonata assemblages; (ii) to understand if mixed artificial and natural habitat landscapes support greater nestedness than homogeneous habitat landscapes (only artificial or only natural systems); iii) to figure out if some selected environmental factors and species traits may be responsible for such a pattern and (iv) to stress the possible role of artificial habitats

in ecosystem management and conservation for Odonata and other aquatic insects.

Materials and methods

Study area and sampling activity

The Castelporziano Presidential Estate, a nature reserve along the Tyrrhenian coast near Rome, is a 60 km^2 well-conserved patch of both wet and xeric pristine woodlands in a Mediterranean climatic zone where several species of Odonata breed in numerous small ponds and pools (Manfredi Frattarelli et al. 2012). Although there are no permanent superficial running waters, several seasonal ponds and pools are widespread where soil depressions allow rainfall to collect, and twenty drinking troughs built for free-ranging cattle watering are scattered across the estate (Domeneghetti et al. 2015). Drinking troughs are brickwork tanks on average 4–10 m long, 1–1.5 m wide, 0.5–0.6 m deep, often artificially kept full of water all over the year for cattle beverage. They are often colonized by some animal taxa, especially aquatic invertebrates (insects, crustaceans, mollusks, etc.) that generate flourish communities, given the absence of top predator like fishes.

In a previous paper (Domeneghetti et al. 2015), a good qualitative field survey of the adult Odonata community of the Castelporziano Estate was conducted with a standardized sampling of 18 pools. Therefore, we decided to supplement those data, focusing instead on the previously unsampled drinking troughs of the estate. The sampling period went from December 2017 to June 2018. We surveyed all drinking troughs present in the study area. We decided to focus on the ultimate or penultimate larval stage specimens of Odonata (easier for taxonomic identification) to avoid the bias of adult dragonflies that fly over water bodies but do not deposit eggs and do not effectively belong to the site community. To collect Odonata species in the drinking troughs, we sampled the water body space by using simultaneously two landing nets ($60 \times 50 \times 50$ cm; 6 mm mesh) covering all the trough volume along the trough length (Cerini et al. 2019) for three consecutive sampling sessions. All the collected detritus and algae were inspected, and all macroinvertebrates were hand-collected and put in plastic boxes. All the Odonata larvae were identified; the species which were unsure of were collected in alcohol 95% for microscope analysis and identification by using the most updated key identification guide for Italian dragonfly species (Carchini 2016). Every trough was geo-referenced using a GPS device (data for pools were already present in Domeneghetti et al. 2015, Fig. 1); for each water body we estimated the area (m^2) and an isolation index (m: distance from the closest water
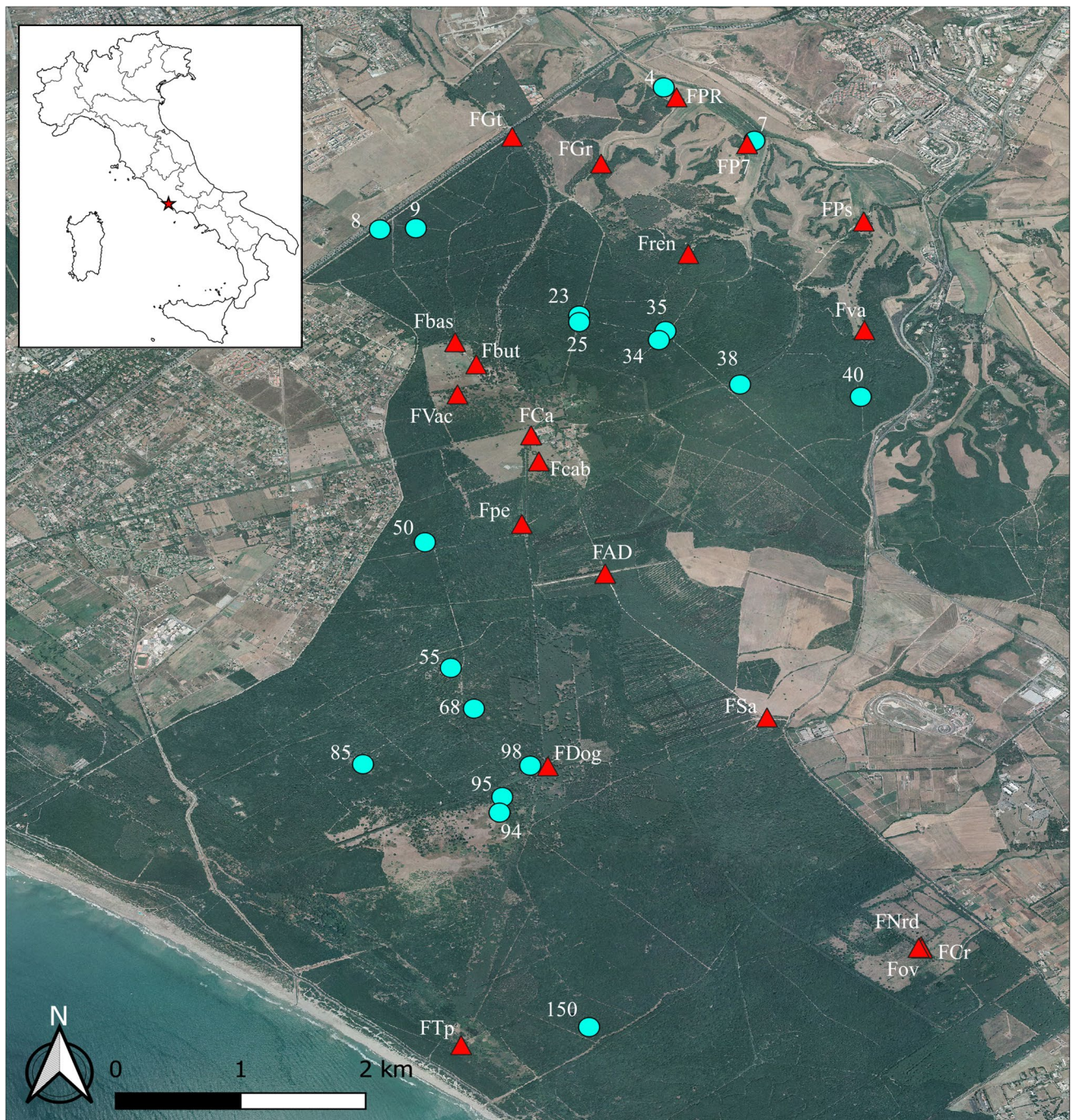
Fig. 1 Geographical placement of the study area in Italy and sites location with labels: circles represent pools; triangles represent drinking troughs

body). Moreover, since the dispersal ability of the species could influence the assemblage nestedness pattern, we consulted the literature data of wing span and body length (Siesa 2017) as proxy of the specific dispersal ability: larger measurements of such traits can be correlated to longer dispersal capacity (Murakami and Hirao 2010). We further evaluated the habitat use of species along the

ecological generalism/specialism gradient by assigning a value between 1 (highly specific) to 6 (generalist) to each species based on the most updated field guide for Italian Odonata (Siesa 2017). We evaluated the commonness of the species, the indication of population densities and the number of habitat types where the species is found.

Statistical analyses

We organized the literature data (Domeneghetti et al. 2015) and our sampling data in binary presence-absence matrices with sites as columns and species as rows. We created three matrices: one containing only the drinking troughs data, one with the natural pools data, and a mixed one with all data together. For measuring nestedness, we used two of the most used metrics: the NODF (nestedness measure based on overlap and decreasing fills, Almeida-Neto et al. 2008) and the matrix temperature (T; Atmar and Patterson 1993; Rodríguez et al. 2006). NODF quantifies independently (1) whether depauperate assemblages constitute subsets of progressively richer ones and (2) whether less frequent species are found in subsets of the sites where the most widespread occur. The T metric is based on distances of unexpected presences and absences from a diagonal isocline of perfect nestedness, therefore testing for an aggregate pattern that reflects both species incidence and species composition. The two metrics were compared with 500 null matrices to calculate Z-scores and RN scores (relative nestedness) using the "Proportional column and row totals" algorithm (Strona and Fattorini 2014), in order to assess the significance of the measured nestedness. With this algorithm the column and row totals of the simulations do not all match the totals of the empirical matrix, although overall both matrix fill and the matrix dimensions are kept constant. The "Proportional column and row totals algorithm" is more ecologically realistic, especially in the context of habitat islands and small patches as stochastic temporal variation in habitat richness and species incidences (Matthews et al. 2015), thus matching our ecological context of temporary and permanent water bodies. Additionally, this model is most suited to a small-scale analysis (Ulrich and Gotelli 2012), like our 60km² total area and small artificial sites. We used the online tool Ned for analysis (https://ecosoft.alwaysdata.net/; Strona et al. 2014). The study sites and species were ordered by packing the matrix for maximum site nestedness. To evaluate the influence of site area, isolation, and dispersal ability on the assemblage nestedness we then compared the nestedeness site order to the area and degree of isolation orders of the study sites by means of Spearman's rank correlation. Then we correlated the nested species order to the rank of proxies of species dispersal ability (wing span and body length). We correlated the nested species order to the generalism/specialism species habitat use order with Spearman's rank correlation (Schouten et al. 2007). We performed correlations for all the dataset (trough, pool and mixed systems) after maximum nestedness packing. Finally, we tested the difference between species richness between natural pools and drinking troughs by means of Mann–Whitney U Test.

Results

We explored 20 drinking troughs widespread within the Castelporziano Estate. Four out of 20 troughs were found empty of water or without Odonata. The "Pools" matrix comprised 24 species and 18 sites (natural pools), while the "Troughs" matrix contained 10 species in 16 sites (artificial drinking troughs) (Tables 1, 2). A total of 25 species (13 Anisoptera, 12 Zygoptera) and 34 sites (18 natural pools, 16 drinking troughs) comprised the "Mixed" matrix. The ratio of the areas of the largest and smallest sites was higher in the mixed landscape (525) than in natural (49) and artificial (8.9 after removing the lowest outlier) landscapes (Area values in Table 1). Estimated species richness in natural pools was significantly higher than average richness in drinking troughs (U = 49.5, p < 0.01 Mann–Whitney U Test): maximum and minimum richness for natural habitat was respectively 15 and two species with median richness of 6.50; for artificial habitats it was respectively six and one species with median richness of 2.50. Odonata found in the drinking troughs represented 40% of the whole species pool found in the study area (Table 2). The Odonata assemblages within natural and artificial water bodies were significantly nested with both NODF and T metrics, while for NODF both columns and rows (sites and species) resulted

Table 1 Sites summary table: information for natural pools and drinking troughs with reference to their label in the map, surface area [Area (m²)] and distance from the closest waterbody [Isolation (m)]

Pools			Troughs		
Label	Area (m²)	Isolation (m)	Label	Area (m²)	Isolation (m)
85	4470	1100	Fdog	76	140
7	4113	75	FVac	38	385
4	3599	155	Fbas	35	312
95	2027	175	Fpe	35	812
150	1268	2617	FPs	31	1267
55	1020	525	Fva	27	772
94	953	175	FPR	23	155
40	840	772	Fov	23	2800
35	451	100	FNrd	23	2800
34	371	100	FCr	23	2800
68	313	525	Fcab	22	753
9	300	287	Fren	21	932
38	215	837	FGr	16	972
50	188	812	FP7	10.5	75
25	175	90	Fbut	8.5	312
23	170	90	FAD	0.65	877
98	160	140			
8	91	287			

Broken or dry troughs were not included

Table 2 Species summary table: information on the species, their taxonomic Order, the maximum body length (mm), the posterior wing maximum span (mm), the habitat specificity value between 1 (highly specific) to 6 (generalist) (Siesa 2017) and the presence in troughs, pools or in both the habitat types

Species	Order	Body length	Wing span	Habitat specificity	Presence
Calopteryx haemorrhoidalis	Zygoptera	48	27	2	Pools
Chalcolestes sp.		48	28	3	Pools
Lestes barbarus		45	27	4	Pools
Lestes virens		39	24	3	Pools
Sympecma fusca		39	22	4	Pools
Ischnura elegans		34	21	5	Pools, Troughs
Coenagrion puella		35	24	5	Pools
Coenagrion scitulum		33	20	2	Pools
Erythromma viridulum		32	21	2	Pools
Erythromma lindenii		36	21	3	Pools
Ceriagrion tenellum		35	21	4	Pools
Platycnemis pennipes		37	24	3	Pools
Aeshna mixta	Anisoptera	64	42	3	Pools
Aeshna affinis		66	42	4	Pools
Anax imperator		84	52	4	Pools, Troughs
Anax parthenope		75	51	3	Pools
Libellula depressa		48	38	6	Pools, Troughs
Orthetrum cancellatum		50	41	6	Pools, Troughs
Orthetrum coerulescens		45	34	5	Pools
Orthetrum brunneum		49	38	6	Troughs
Crocothemis erythraea		45	33	6	Pools, Troughs
Sympetrum striolatum		44	30	5	Pools, Troughs
Sympetrum fonscolombii		40	30	5	Pools, Troughs
Sympetrum sanguineum		39	29	5	Pools, Troughs
Sympetrum meridionale		40	30	5	Pools, Troughs

in a significantly nested pattern, except for the species of "Troughs" matrix (Table 3). Notably, the statistical significance of nestedness observed in the mixed system was larger (higher Z-scores; Table 3) than in the single systems, that is: mixed artificial and natural habitat landscapes supports greater nestedness than homogeneous habitat landscapes. A close inspection of the "Mixed" matrix packed to maximal nestedness (Fig. 2), revealed that half of the drinking troughs were interspersed with the natural pool, while the remaining half clustered at the right end of the packed matrix. No significative effect between the environmental variables and the species trait ranking with the nested order of species and sites was found for the "Pools" and the "Troughs" matrices. Only the relationship between the area order of the Pools and their nested order nearly reached the significance ($r = 0.46$, $P = 0.054$). As for the "Mixed" matrix, there was a significant effect of the size and isolation parameters on nestedness. Nested site order correlated positively with site area order ($r = 0.63$, $P < 0.001$) and negatively with site isolation order ($r = -0.593$, $P < 0.001$; Fig. 3b, c). The biggest and smallest natural pools areas were respectively 4470 m^2 and 91 m^2, whereas the drinking troughs areas were 76 m^2 and 0,65 m^2. As for isolation metric, the most isolated natural

Table 3 Nestedness metrics (NODF, and T; Null Model: Proportional column and row totals) estimated at the study Odonata assemblage, with calculation of Z-score and RN (relative nestednes) indices

Metric	Index	Z-score	RN	Nested?	Matrix
NODF	45.159	9.824	0.706	Yes (p < 0.001)	Mixed
NODF_row	43.894	9.457	0.685	Yes (p < 0.001)	
NODF_col	45.836	9.833	0.727	Yes (p < 0.001)	
T	14.701	−6.071	−0.621	Yes (p < 0.001)	
NODF	48.749	5.894	0.440	Yes (p < 0.001)	Pools
NODF_row	50.395	5.665	0.489	Yes (p < 0.001)	
NODF_col	47.836	5.529	0.414	Yes (p < 0.001)	
T	26.559	−3.652	−0.413	Yes (p < 0.001)	
NODF	48.74	2.436	0.292	Yes (p < 0.01)	Troughs
NODF_row	49.792	2.562	0.317	Yes (p < 0.01)	
NODF_col	45.937	1.630	0.225	No (p > 0.05)	
T	27.743	−2.081	−0.339	Yes (p < 0.05)	

The last column indicates where a significant difference in the metrics of nestedness between the real matrix and the simulated null communities. A "Yes" stands for a significant nested pattern, followed by p value. Results are showed for the mixed matrix containing both natural and artificial habitats, for the natural pools matrix and for the drinking troughs matrix separately
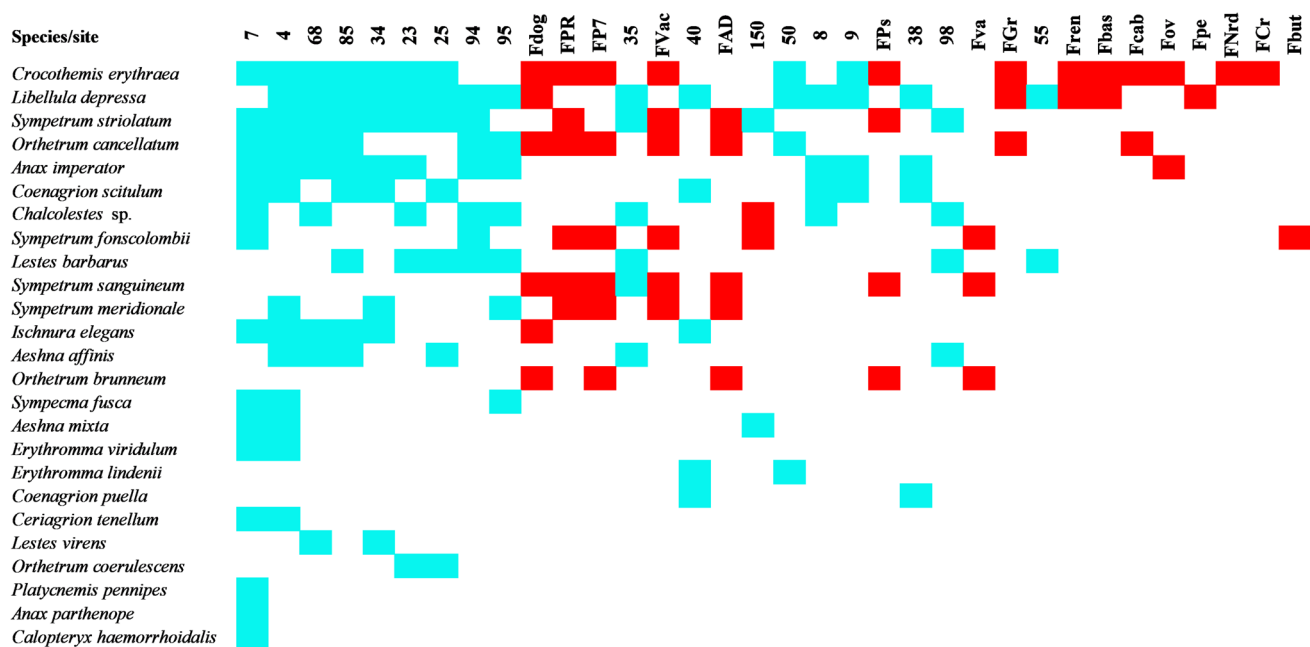
Fig. 2 Matrix of sites and species arranged according to maximum nestedness. Sites name starting with F represent drinking troughs (Red squares), sites name that are only numbers represent natural pools (pale blue). A red or pale blue cell represents a presence of the species. (Color figure online)

pool (150. Figure 1) was 2617 m distant from any other water body, whereas among drinking troughs, FCr, FNrd and Fov (Fig. 1) were 2600 m far from the closest water body. The wings span and body length order of the species showed no significative correlation with nestedness, while there was a positive correlation of the nested species order to the species generalism ($r = 0.578$, $P = 0.002$; Fig. 3a).

Discussion

Overall, we found a nestedness arrangement of the Odonata assemblages in the considered systems (i.e. natural, artificial and mixed aquatic habitats), with the highest nestedness degree observed in the mixed landscape. The observed nested pattern can be interpreted from both environmental and species' ecology perspectives. It is noteworthy that significant effects of the habitat and species traits gradients on the nestedness arrangement arose only from the system consisting of interspersed natural and manmade waterbodies, thus suggesting that such a mixed landscape presented emerging properties in comparison to the homogeneous landscapes alone. Moreover, the small artificial aquatic habitats can host Odonata assemblages richer than those from larger natural pools. Indeed, drinking troughs play a non-marginal role in supporting Odonata diversity in a seminatural landscape composed by a mosaic of natural and manmade waterbodies.

The higher significance of nestedness observed in the mixed landscape can be attributable to the positive effect on nestedness by the ratio of the areas of the largest and smallest sites (Wright et al. 1997), this being smaller in the homogeneous landscapes than in the mixed (525). As for the possible drivers of nestedness, the drinking troughs showed a lack of correlation between the nested order and the environmental and species rankings. This result could be anticipated given the high similarity of features of such habitats and the tendency to be colonized mostly by the most generalist species. More surprisingly is the absence of correlation between habitat and species traits rankings to the nestedness in natural pools. Probably the nested pattern is driven by other factor not considered in the present study. As for the mixed habitat system, our analyses revealed interesting patterns. From the environmental perspective, two features, site area and isolation, may explain the observed Odonata community arrangement. The effect of site size on nestedness was expected since "the larger is area, the higher is the species richness" is a very well-known and validated rule in ecology (Wilson and MacArthur 1967; Connor and McCoy 1979; Samuel et al. 2000; Steffan-Dewenter 2003). Also, the site isolation correlated well with the nested sites order, the more isolated sites being also the poorer as for richness, albeit showing an idiosyncratic relationship with the species dispersal capability data. Indeed, from the species ecology perspective, the dispersal capability apparently does not correlate with the nested species order, that is: species assumed
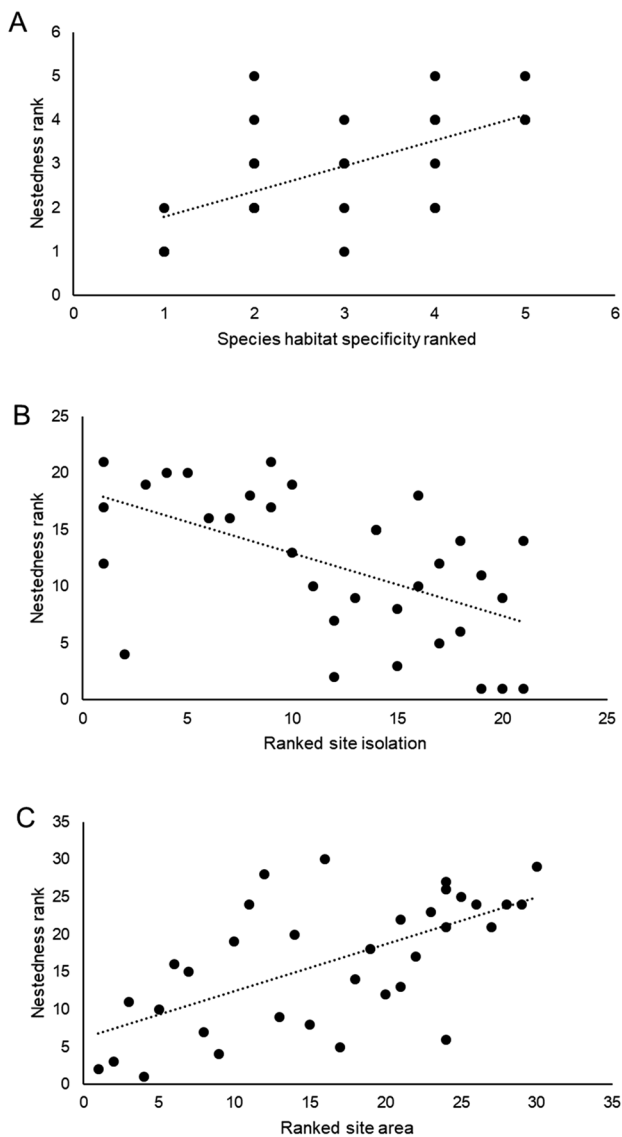
Fig. 3 Scatterplots of the statistical significative correlations. **a** Species ranked by their nested pattern (commonness) plotted against species ranked by habitat specificity values (from the more specialist to the more generalist). **b** Sites ranked by their nested pattern (species richness) plotted against sites ranked by isolation values (from the less isolated to the more isolated). **c** Sites ranked by their nested pattern (species richness) plotted against sites ranked by area values (from the smaller to the larger)

to have higher flight capacity are not the commonest species, and possibly do not colonize the more isolated sites. Although this result does not support our expectations that more isolated sites are more unlikely to be colonized for species with low dispersal ability (Cutler 1994), the relatively small extension of our study area (60 km^2) makes even low-vagile species potentially capable of covering the distance separating the farthest sites (2.8 km) (Corbet 2004; Suhling et al. 2017). Overall, the habitat preferences by species (i.e.

generalism vs. specialism ecological continuum) appears to be a more important factor driving the nestedness observed. The strong relation between generalism rank and nested species order confirmed that more generalist species tends to be also the commonest in our wetland network. The sites composed by progressively less species are inhabited by the more common and euriecious species [i.e. *Crocothemis erythraea* (Brullé, 1832) and *Libellula depressa* Linnaeus, 1758]. Such pattern mirrors the results of another study where the differences in habitat preference between the rare and common species drove the positive effect of some environmental variables (i.e., forest cover, aquatic vegetation) on the nested pattern in Odonata (Sakai et al. 2017). Thus, nestedness analysis may help in identifying habitat features that should be considered for conservation of rare (or threatened) species and for restoration of lentic habitats (Sakai et al. 2017).

An interesting pattern emerging from our study is the interspersion of drinking troughs with the natural pools in the nested order (Fig. 2). Indeed, eight artificial sites were richer in species than some natural pools, even though the larger drinking trough is smaller in size (83%) than the smallest pool. Moreover, the smallest drinking trough (0.65 m^2) hosted more species (N = 5) than the smallest pool (91 m^2; N = 4). This shows that in our study system the area of the water body may do not represent a main constraint for species to oviposit and for larvae to grow. Notably, one species [e.g. *Orthetrum brunneum* (Fonscolombe, 1837)] was found exclusively in artificial habitats Therefore, these artificial habitats can be very important for species maintenance because, despite their low extension, they represent small "islands" supporting viable demes of Odonata (and likely other aquatic invertebrates) also during dry periods when most natural water bodies dry out (Manfredi Frattarelli et al. 2012). Indeed, except for sporadic cleaning events, the drinking troughs remain stable throughout the year, as they are continuously filled with running water, and here Odonata larvae limit the risk of drying and predation by top predators (i.e. fishes; Corbet 2004) as usually occurs in natural pools. Notably, changes in the hydroperiod of non-permanent ponds may favour habitat-generalist taxa (nested partitioning of β-diversity among hydroperiods) with a reduction in specialist species (Pires et al. 2017); this enhance the value of drinking troughs in temporary habitats networks to balance this diversity shift by increasing the availability of permanent waterbodies. Moreover, most drinking troughs lack fishes, thus avoiding their possible role as "ecological traps". Other habitats related to human activities, like fishponds, act as ecological traps for Odonata, because they attract adults for ovipositon but do not allow the persistence (subsequent development) of the species due to the predatory pressure exerted by fish. This may represent a threat especially for endangered species (Šigutová et al. 2015).

The importance of artificial habitats (drinking troughs) was already highlighted by Garcia-Gonzalez and Garcia–Vazquez (2011) who assessed how, in the absence or decline of natural ponds and other water points, they can be considered refuges for amphibians, despite their small area. We believe that in the same way troughs can be important for Odonata conservation. The interspersion of such artificial habitats within the natural habitats in a nested fashion strongly supports this hypothesis. Focused management actions on aquatic habitats such as moderate cleaning and protecting vegetation and bottom sediments have been already highlighted as fundamental in the conservation planning of threatened Odonata (Harabiš and Dolný 2015). Same actions performed for drinking troughs can enhance the microhabitat stability and suitability for diverse lentic water species, especially those more linked to/associated with aquatic vegetation, such as many Zygoptera (Askew 1988; Corbet 2004), diving beetles (Coleoptera: Dytiscidae, Franciscolo 1979; Yee 2014) Ephemeroptera and Trichoptera (Grandi et al. 1960; Gee et al. 1997).

In conclusion, our study demonstrates the role of drinking troughs as a complement of natural environments and their potential in elemental implementation of pristine water body networks.

Author contributions The work is all original and the research was carried out by the authors; all authors agree with the contents of the manuscript and its submission to the journal; no part of the research has been published in any form elsewhere; the manuscript is not being considered for publication elsewhere; any research in the paper not carried out by the authors is fully acknowledged in the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The work is compliant with the Ethical standards of Journal of Insect Conservation. The research does not involve protected animals.

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