

## Article

# Niche Partitioning at Emergence of Two Syntopic Dragonflies

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**Abstract:** We investigated the ecological requirements in the emergence phase of two congeneric species of Aeshnidae, *Aeshna grandis* (Linnaeus 1758) and *A. juncea* (Linnaeus 1758), occurring in syntopy at the southernmost limit of their range. We sampled the exuviae of the two species at the peak of their emergence in three lakes in NW Italy. In each lake we defined 30 to 50 sampling plots along the lake borders where we checked for the presence of exuviae and collected data on the microhabitat composition. By modeling the response of the exuviae presence and abundance against the environmental parameters, we could highlight a partial differentiation in the ecological requirements of the two species at emergence. In particular, *A. grandis* is more influenced by the structure of the aquatic vegetation than *A. juncea* and the niche space occupied by *A. grandis* is wider, almost totally encompassing the one of *A. juncea*. We argue that *A. grandis* exploits microhabitats rich in aquatic plants to avoid competition with *A. juncea*. We suggest the preservation of well-structured aquatic vegetation as a key management practice to preserve the three studied populations of *A. grandis*, a species which has been recognized as Vulnerable for Italy according to the IUCN criteria.

**Keywords:** Aeshnidae; n-dimensional hypervolume; ecological niche; species coexistence; Odonata



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## 1. Introduction

The ecological niche of a species consists in the range of ecological conditions in which it can maintain viable populations [1]. However, coexistence of multiple species with very similar ecological requirements may translate into strong competitive interactions, especially when species are phylogenetically related and share similar life history traits [2]. The investigation of local environmental conditions is thus pivotal to explain species coexistence and competition for space and resources [3,4]. While examining ecological factors determining species coexistence in low dispersive organisms can be rather simple [5–10], analyzing the ecological niche in highly dispersive organisms with complex life histories, such as dragonflies, is a task far from trivial [11,12].

Dragonflies are predator insects that spend their entire larval life underwater until they reach the last larval stage; at that point, they move from the aquatic to the terrestrial environment to perform the ecdysis and become adults [13]. As a consequence, the niche requirements of the aquatic larvae are different from those of the terrestrial adults [14], being also more restricted and specialized [15]. The ecological niche of dragonflies can therefore be more easily defined on the basis of the larval requirements to unravel the ecological mechanisms that enable the coexistence of multiple species and the environmental characteristics that enhance the population survival [15]. In this context, the presence of exuviae, namely the final larval exoskeleton left by the emerged adult onto riparian structures, represents an indirect evidence of breeding success within a site, being the only proof of life-cycle completion [16]. It can be used either to monitor the status of threatened

species [17] or to outline ecological requirements during the emergence phase, especially in large-sized species of aquatic invertebrates [18,19]. Thus, using the presence of exuviae as a proxy of site occupancy allows for overcoming the intrinsic uncertainty in examining the ecological preferences of highly dispersive organisms.

As emergence occurs at the water–land interface, both aquatic and terrestrial habitat characteristics are important [20–22]. However, information on the potential niche overlap of phylogenetically-related coexisting species in the emergence phase is extremely scarce. Until now, studies on the selection of emergence sites have been conducted on single species [23–25], while most studies on the ecological niches of coexisting species have focused more on temporal rather than spatial segregation. Considering larvae, in most cases a spatial segregation was observed [26,27], while a temporal separation in the emergence patterns occurs when several congeneric species coexist in the same habitat [28–30]. For instance, two congeneric species, *Anax imperator* Leach 1815 and *A. parthenope* Sélys 1839, share similar environmental requirements but avoid competition through a temporal shift of their emergence peak [31]. However, the spatial segregation of coexisting phylogenetically-related species in the emergence phase has never been examined so far.

Here, we investigated the ecological requirements in the emergence phase of two congeneric species of Aeshnidae, namely *Aeshna grandis* (Linnaeus 1758) and *A. juncea* (Linnaeus 1758), occurring in syntopy at the southernmost limit of their distribution range. Both species have a long life-cycle, as *A. grandis* is semivoltine and *A. juncea* is partivoltine [13], with a number of instars that can vary from 9 to 12 [32]. The last instars are similar in their morphology and dimensions, being around 4–4.5 cm in length, suggesting potential competition [32,33]. Although widely distributed with abundant populations in central and northern Europe [34], on the southern slope of the Alps these species are restricted to high mountain lakes [35] where they likely have to compete for resources. By examining the environmental factors determining the presence of their exuviae, we aimed at determining whether there is overlap in the ecological requirements of the two species during the emergence phase, thus suggesting potential exploitative competition. In particular, we hypothesized that (1) the vegetation structure is a key factor for the emergence site selection, and (2) the two species are in competition for the choice of the best emergence sites because (3) the ecological requirements at emergence of the two congeneric species broadly overlap.

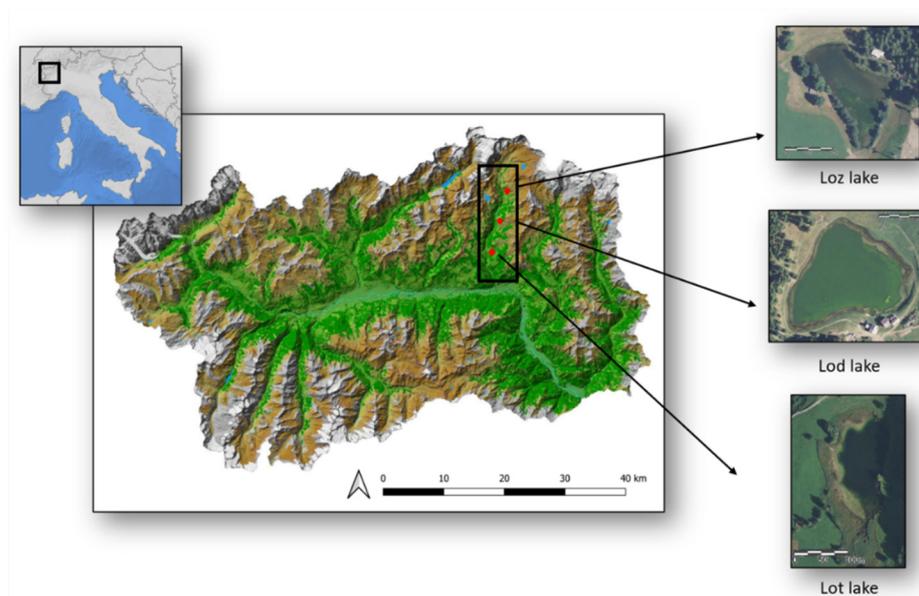
## 2. Experimental Section

### 2.1. Sampling Area

We selected three sampling sites with sympatric populations of *Aeshna grandis* and *A. juncea*, namely Lot, Lod and Loz lakes, all located in the Valtournenche valley within the Val d’Aosta region (NW Italy) (Figure 1). The three lakes are at different altitudes and differ in terms of surface, physical–chemical parameters and vegetation structure (Table 1). The Lot lake is characterized by the presence of a thick layer of vegetation along its banks, mainly *Phragmites australis*, and is surrounded by wet grasslands. The Loz lake is rich in aquatic vegetation, mainly composed of *Juncus* spp., while the Lod lake has scarce aquatic vegetation consisting of few floating macrophytes.

**Table 1.** Details of the three study sites involved in the study. For each lake, we report the municipality, the coordinates (latitude and longitude), the altitude, the surface, the mean water temperature in August and pH (temperature and pH data refer to 2008 and are provided by the Regional Protection Agency of the Val d’Aosta region, <https://www.arpa.vda.it>).

Scheme 2	Municipality	Latitude	Longitude	Altitude (m)	Surface (m <sup>2</sup> )	Temperature (°C)	pH
Lot lake	Antey–St.-André	45.802626	7.5942989	1479	15.150	19.0	7.05
Loz lake	Valtournenche	45.890443	7.6290202	1718	8.169	15.8	9.07
Lod lake	Chamois	45.844495	7.620993	2022	16.700	18.0	8.02



**Figure 1.** Map of the three sampling localities in the Val d'Aosta region with aerial pictures of the three lakes (<https://geoportale.regione.vda.it>).

## 2.2. Sampling Design

Samplings were performed in summer 2014, during the last week of August, which represents the peak of emergence of both species according to our previous observations in the area [36]. Although the emergence phase of the two examined species in the study area is comprised between June and August, we here decided to focus on the emergence peak of the two species. This approach allowed us to disentangle the potential spatial niche overlap during this phase. We tried to perform our samplings at least one week after the last rain event to avoid any sample bias due to the loss and destruction of exuviae caused by rain. For each sampling site, we randomly identified 30 to 50 sampling plots, consisting of circles with a diameter of 1 m, placed along the perimeter of each lake at the interface between water and land. In each sampling plot we collected all exuviae belonging to Aeshindae. Exuviae were preserved in 70% ethanol in a separate falcon tube for each plot, and subsequently determined in the laboratory [32,33]. In each sampling plot we also measured 10 environmental variables, potentially important for the emergence of dragonflies. By positioning ourselves at the center of the plot, we first measured the distance from the water line (water distance), the water depth (water depth) and the average height of aquatic vegetation from water surface (vegetation height) with a tape meter. We then estimated both aquatic and terrestrial parameters by evaluating the percentage of coverage of: water (%water cover) that encompasses both the clear water and the water covered by vegetation; shoreline plants, e.g., *Typha* spp. and *Juncus* spp. (%shoreline plants); aquatic plants, e.g., *Nuphar luteum* and *Lemna minor* (%aquatic plants); terrestrial plants (%terrestrial plants); trees and shrubs (%tree and shrubs); and bare soil (%bare soil) (see [37] for the definition of plant categories). Finally, we estimated the percentage of canopy cover (%canopy cover) of the plot (see Table S1 for the values of environmental variables in each sampling site).

## 2.3. Statistical Analyses

We performed all statistical analyses in R [38].

### 2.3.1. Generalized Linear Mixed Models

First, we performed data exploration [39] to evaluate the potential for a confounding effect of multicollinearity among predictors using variance inflation factors (VIFs) and the Pearson correlation test ( $VIF < 2$  and  $|r| < 0.5$ ). We then graphically checked for

potential nonlinear relationships between covariates and outliers. In order to test the main environmental factors influencing the number of exuviae of *Aeshna grandis* and *A. juncea*, we performed generalized linear mixed models (GLMMs) with the “lme4” package for R [40]. Given the high number of zeros in our dependent variables, we applied a zero-inflation procedure by performing two separate sets of models on: (i) presence/absence data and (ii) count data excluding the zeros. We assumed a Poisson distribution using a log-link function for the count data, and a Bernoulli distribution for the presence/absence data, with the complementary log-log link function (clog-log) for data with unbalanced sets of zeros (absences) and ones (presences) [41]. The lake identity (LakeID) was included in the models as a random factor to account for spatial autocorrelation. The abundance of exuviae belonging to the potential competitor species, i.e., the number exuviae of *Aeshna grandis* for *A. juncea* and the number of exuviae of *A. juncea* for *A. grandis* (No. exuviae), were also included in the models to test for a direct competition among the two species. Model selection occurred with a backward elimination, progressively excluding variables which caused an increase of the AIC value; we then validated the final models by plotting the residuals against predictor variables [39].

In accordance with the results of data exploration, we selected seven predictor variables to be included in the regression models, namely water depth (water depth), height of riparian vegetation (vegetation height), percentage of canopy cover (%canopy cover), percentage of water cover (%water cover), percentage of shoreline plants (%shoreline plants), percentage of aquatic plants (%aquatic plants), percentage of bare soil (%soil) and the number of exuviae of the potential competitor (No. exuviae). The percentage of trees and shrubs (%trees and shrubs) and the distance from the water line (Water distance) were excluded due to the high number of zeros in their distributions (see Figure S1), while the percentage of terrestrial plants (%grass) was excluded due to collinearity with the percentage of shoreline plants (%shoreline plants).

### 2.3.2. Hypervolume Analysis

In order to check for overlap in the microhabitat selection of the two species, we reconstructed the environmental n-dimensional hypervolume occupied by each species with the “hypervolume” R package [42] with a Gaussian kernel density estimator [43]. We constructed the n-dimensional hypervolume for both *Aeshna juncea* and *A. grandis* on the basis of the variables retained in the final selected GLMM models (see previous paragraph). We rescaled all variables before the analysis, in order to achieve the same dimensionality for all axes in accordance with the assumptions of the hypervolume construction [44]. We standardized the choice of bandwidth for each variable through a Silverman estimator and we set a threshold that included 100% of the total probability density. We characterized each niche by calculating total hypervolume volume, dispersion and evenness [45] using the functions *kernel.alpha*, *kernel.dispersion* and *kernel.evenness* implemented in the “BAT” R package [46]. We then assessed pairwise niche differentiation among hypervolumes of the four species using the distance between centroids and the overall similarity (i.e.,  $\beta$ -diversity), as implemented in the function *kernel.beta*. Furthermore, overall differentiation ( $\beta_{tot}$ ) was decomposed into its two additive components, namely: (i) the replacement of space between hypervolumes ( $\beta_{repl}$ ), which reflects niche shift processes; and (ii) net differences between the amount of space enclosed by each hypervolume ( $\beta_{rich}$ ) that measures variations in niche volume of one species with respect to the other (i.e., expansion or contraction) [47].

## 3. Results

We identified a total of 118 plots encompassing the three sampling sites and we retrieved a total of 266 exuviae belonging to Aeshnidae, among which 82 were identified as *Aeshna grandis* and 144 as *A. juncea* (Table 2).

**Table 2.** Number of plots for each site and number of collected exuviae, mean and standard deviation (in brackets) for each species in the three sampling sites.

Scheme	Total Plots	<i>Aeshna grandis</i>		<i>Aeshna juncea</i>	
		N Exuviae	Mean ( $\pm$ SD)	N exuviae	Mean ( $\pm$ SD)
Lot lake	30	31	1.03 ( $\pm$ 1.33)	17	0.57 ( $\pm$ 0.90)
Lod lake	50	23	0.46 ( $\pm$ 0.76)	95	1.90 ( $\pm$ 2.41)
Loz lake	38	28	0.74 ( $\pm$ 1.39)	32	0.84 ( $\pm$ 1.78)

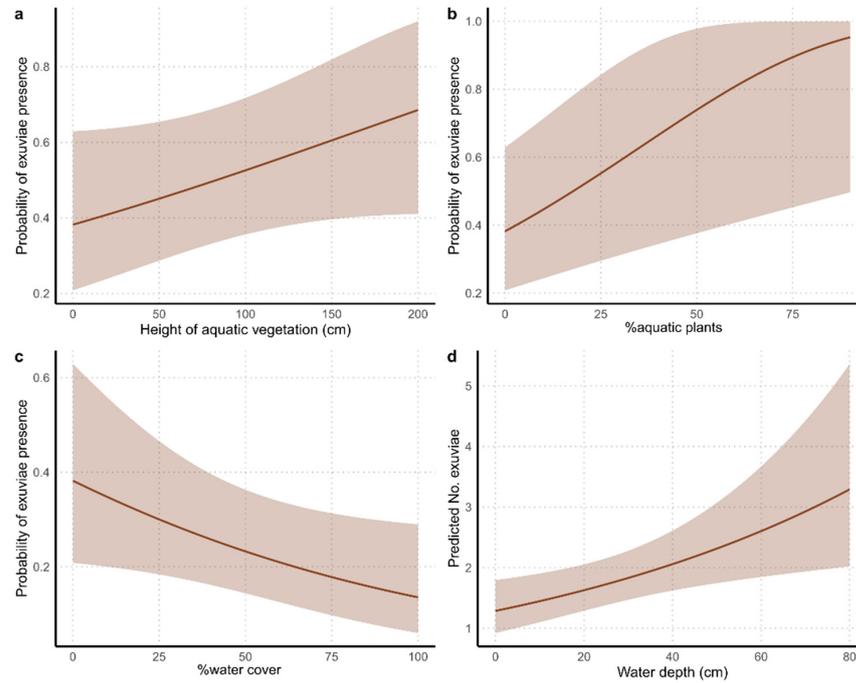
The results of the final selected models showed that the probability of site choice by *Aeshna grandis* for emergence was positively influenced by the percentage of aquatic plants and vegetation height, whereas the percentage of water had a negative effect (Table 3a and Figure 2a–c). Within the microhabitats suitable for the emergence of *A. grandis*, greater water depth significantly increased the probability of finding exuviae in the plot (Table 3a and Figure 2d). Conversely, the probability of site choice by *A. juncea* for emergence was positively influenced by the percentage of canopy cover and water depth, while it was negatively affected by the percentage of water (Table 3b and Figure 3a–c). Although not significant, the percentage of shoreline plants was included in the final model according to the model selection procedure. Within the microhabitats suitable for the emergence of *A. juncea*, high percentages of canopy cover significantly increased the probability of finding exuviae in the plot (Table 3b and Figure 3d). The number of exuviae of the potential competitor species (No. exuviae) was excluded in all models.

**Table 3.** Estimated parameters ( $\beta$ ), standard errors (SE), z-values (Z) and p-values (P) for each covariate and the intercept in the final selected models for the presence/absence and count data of *Aeshna grandis* (a) and *A. juncea* (b). Significant values are highlighted in bold.

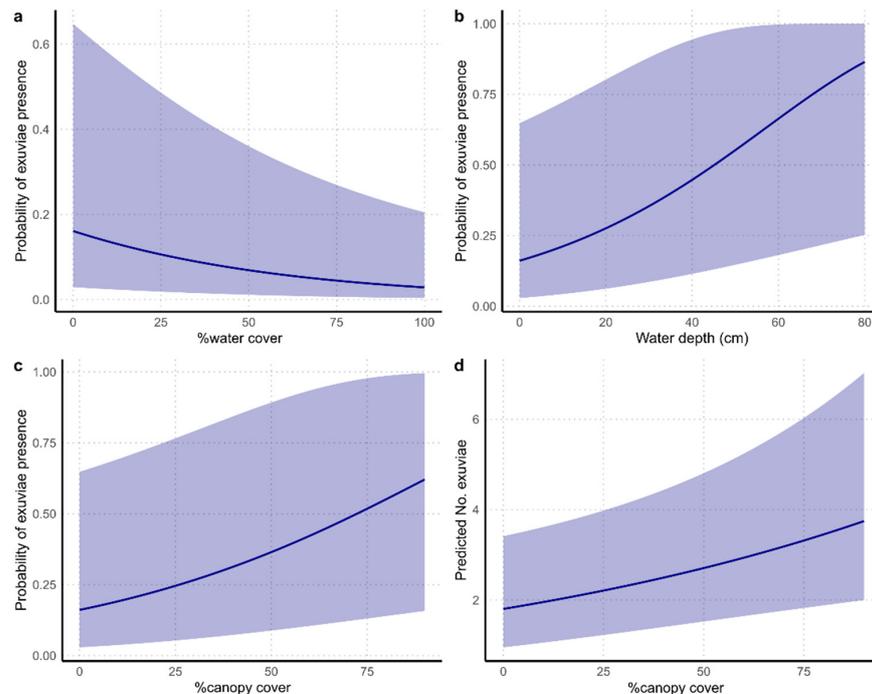
Variable	Presence/Absence Data				Count Data			
	$\beta$	SE	Z	P	$\beta$	SE	Z	P
<b>(a) <i>Aeshna grandis</i></b>								
Intercept	−0.731	0.369	−1.98	<b>0.047</b>	0.253	0.170	1.49	0.137
%aquatic plants	0.021	0.007	2.940	<b>0.003</b>	-	-	-	-
%water cover	−0.012	0.006	−2.002	<b>0.045</b>	-	-	-	-
Vegetation height	0.004	0.003	1.597	0.110	-	-	-	-
Water depth	-	-	-	-	0.012	0.004	2.680	<b>0.007</b>
<b>(b) <i>Aeshna juncea</i></b>								
Intercept	−1.74	0.909	−1.91	0.056	0.590	0.325	1.82	0.070
Water depth	0.030	0.012	2.455	<b>0.014</b>	-	-	-	-
%canopy cover	0.019	0.008	2.244	<b>0.025</b>	0.008	0.003	2.680	<b>0.007</b>
%water cover	−0.018	0.006	−2.924	<b>0.003</b>	-	-	-	-
%shoreline plants	−0.045	0.026	−1.765	0.078	-	-	-	-

When examining the dimension and overlap of their ecological niches, *Aeshna juncea* showed the smaller five-dimensional hypervolume, while hypervolume dispersion and evenness were similar between the two species (hypervolume dimension: *A. grandis* = 956.5, *A. juncea* = 621.9; hypervolume dispersion: *A. grandis* = 2.77, *A. juncea* = 2.68; hypervolume evenness: *A. grandis* = 0.106, *A. juncea* = 0.089). The measure of similarity showed that the hypervolume of the two species broadly overlapped, as the intersection encompassed 53.7% of the hypervolume of *A. grandis* and 82.6% of the hypervolume of *A. juncea*, while the distance between centroids was low (Intersection = 513.6; Distance between centroids = 0.16). This is supported by the results of the pairwise  $\beta$ -diversity analysis, which showed that half of the total hypervolume was shared between the two species ( $\beta_{\text{tot}} = 0.49$ ). The decomposition of  $\beta$ -diversity into its components highlighted that the differentiation between the ecological niches of the two species was mostly explained by niche contraction ( $\beta_{\text{rich}} = 0.32$ ), while niche shifts played a minor role ( $\beta_{\text{repl}} = 0.17$ ). The overlap between ecological niches (Figure 4) indicated that the unique portion of *A. grandis*

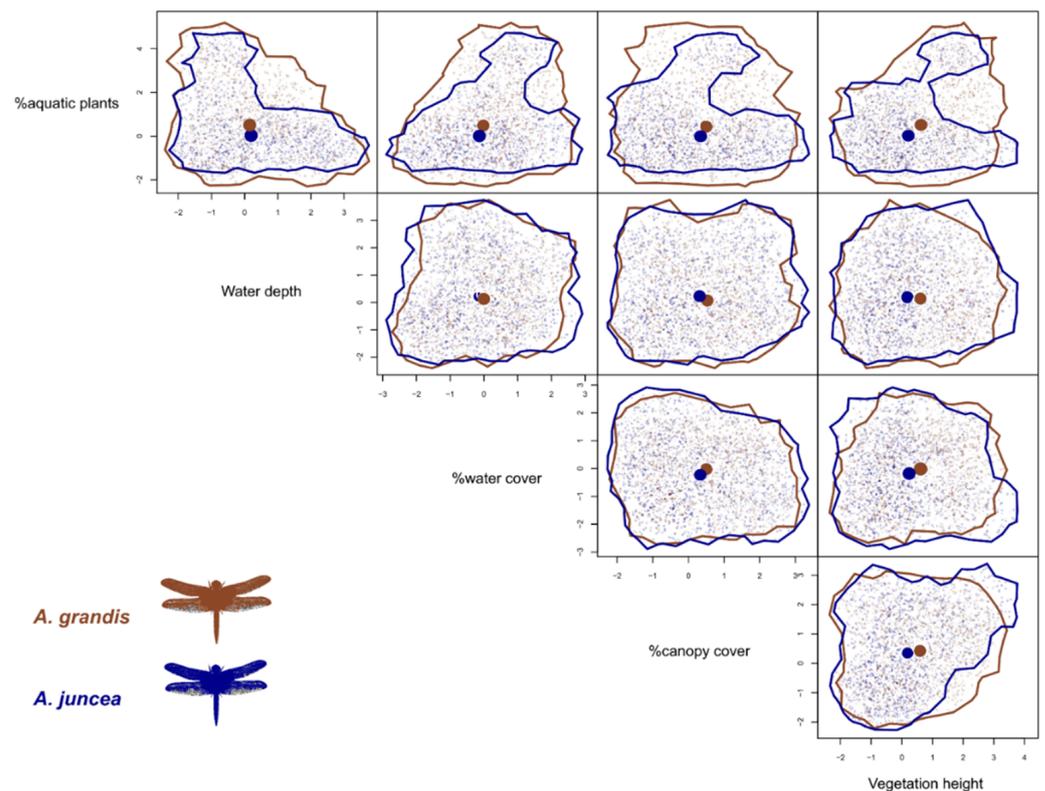
niche was mainly determined by the fact that it exploited microhabitats with high densities of aquatic plants, where the presence of *A. juncea* was limited.



**Figure 2.** Predicted values and confidence intervals for the probability of presence and the number of exuviae of *Aeshna grandis* modeled against significant variables: (a) height of aquatic vegetation (probability of presence); (b) %aquatic plants (probability of presence); (c) %water cover (probability of presence); and (d) water depth (number of exuviae).



**Figure 3.** Predicted values and confidence intervals for the probability of presence and the number of exuviae of *Aeshna juncea* modeled against significant variables: (a) %water cover (the probability of presence); (b) water depth (the probability of presence); (c) %canopy cover (the probability of presence); and (d) %canopy cover (number of exuviae).



**Figure 4.** Pair plots showing the estimated five-dimensional hypervolumes for the two species. The colored points for each species reflect the centroids (large points), and the 1000 stochastic points sampled from the inferred hypervolume (small points). Contour lines are drawn for visual presentation. Variables are rescaled. Pictograms by [Phylopic.org](https://www.phylopic.org/).

#### 4. Discussion

We explored the role of interspecific competition in shaping the ecological preferences and the consequent general geometry of the niche of *Aeshna grandis* and *A. juncea* (Aeshnidae) at the southernmost margin of their range. Our results partially confirmed our initial hypotheses as we could demonstrate, at least in *A. grandis*, the pivotal role of aquatic vegetation in determining the choice of emergence sites. In fact, we showed that this species is favored by higher vegetation and by higher densities of aquatic plants. The positive effect of higher supports for the emergence phase has been highlighted in literature for *Orthetrum cancellatum* (Linnaeus 1758) [48], for *Gomphus lucasii* Selys 1849 [49] and *Onychogomphus costae* Selys 1885 [50]. From an ecological point of view, emergence at higher levels above water may guarantee higher light availability and offer a lower risk of predation from water organisms (e.g., fish, amphibians, other dragonfly larvae); in addition, it provides less competition for the emergence space [51]. Similarly, higher habitat complexity, such as that provided by higher densities of aquatic plants, may reduce mortality rates [52]. For instance, the threatened *Aeshna viridis* Eversmann 1836 requires a particular macrophyte species (the water soldier, *Stratiotes aloides*) in the emergence phase as it provides protection from predators [22,53]. In addition, denser vegetation may offer more emergence substrates, thus reducing overcrowding and providing protection against flying predators (e.g., birds, adult dragonflies) and extreme weather [24].

The role played by the need for protection in the choice of emergence sites partially explains also the significant positive effect of the canopy cover on *Aeshna juncea*. Although limiting the light, canopy cover can provide shelter in the immediate emergence area, thus enhancing protection from predation [21]. In addition, shaded areas are also characterized by cooler and more stable temperatures that may be more suitable for this species. The key role of temperature as a driver of the onset and synchronization of dragonfly emer-

gence has been often pointed out in literature [13,28,54]. Based on these evidences, we can speculate that *A. juncea* requires lower air temperatures for the onset of the emergence compared to *A. grandis*. The temperature requirements also possibly explain the counter-intuitive combined positive effect of water depth and negative effect of water coverage observed for both species. These results suggest that emergence often occurs on the lake borders, but it is favored on deep banks, possibly because daily variations in temperature are reduced in deep waters. In this context, the emergence phase is influenced not only by the temperature at the onset but also by the temperatures experienced by larvae during their development [28]. Deep waters may therefore buffer temperature variations, thus favoring the synchronization in the emergence patterns of the species examined. Although the %water cover is shared among the two species, the intercepts of the statistical models are different, suggesting that they are able to avoid competition even when their ecological requirements overlap. This conjecture is additionally supported by the exclusion of the exuviae abundance of the potential competitor species from the models of both species, which did not support our second hypothesis.

The results of the hypervolume analysis demonstrated that the ecological niches of the two species broadly overlap, thus confirming our third hypothesis. When examining the niche hypervolumes of the two species, we observed that the dimension of the ecological niche of *Aeshna juncea* was considerably smaller, being almost completely nested within the one of *A. grandis*. We can tentatively explain such overlap by interpreting the regression results, pointing at the structure of vegetation, and especially the coverage of aquatic plants, as the main factor determining the segregation of the two species. Although aquatic plants are often preferred by damselflies [29,55], we can hypothesize that this substrate represents a suitable habitat for *A. grandis*: in fact, as demonstrated by a mesocosm experiment, its larvae are able to exploit the rosettes of *Stratiotes aloides* and even outcompete the larvae of the congeneric species *A. viridis* [56]. Based on our results, the preservation of the aquatic vegetation, and especially of aquatic plants, is therefore crucial not only to guarantee the complex habitat structure that favors the emergence of *A. grandis* but also to permit the coexistence of the two congeneric species of Aeshnidae in the investigated sites. Although the coexistence of multiple dragonfly species is often mediated by a temporal segregation in the emergence peaks [28–30], the structure of the vegetation could enhance species coexistence through spatial segregation.

Until now, studies on ecological preferences in the selection of emergence sites by dragonflies have mainly been conducted on single species [20,23,25]. At the same time, the potential niche overlaps among congeneric species coexisting in the same habitat have always been resolved by examining the temporal segregation [27,28,31], even if spatial segregation among *Gomphus flavipes* and *G. vulgatissimum* was observed [30]. In our case, we took advantage of the simultaneous emergence peak of the two coexisting Aeshnidae species to highlight potential spatial rather than temporal segregation. Our approach also allowed us to identify some key management aspects that could be implemented to enhance the conservation of *A. grandis* in these peripheral populations. Whereas this species is classified as Least Concern for Europe [57] and for the Mediterranean basin [58], it has been recently recognized as Vulnerable for Italy according to the criteria of the IUCN, as it is present only in few sites on the southern slope of the Alps [59]. In particular, the three populations examined in this work represent the only three records of *A. grandis* in NW Italy [34]. In this context, our work represents a baseline for the investigation of the ecological requirements of this species and for the consequent implementation of management practices devoted to the conservation of these peripheral populations.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/2673-4133/2/1/2/s1>, Table S1: Measures of environmental parameters, Figure S1: Dotplots to check for outliers, Figure S2: Results of the correlation test to check for collinearity among covariates.

**Author Contributions:** Conceptualization, M.I., E.P. and E.R.; methodology, M.I., E.P. and E.R.; formal analysis, E.P. and S.M.; investigation, M.D. and E.P.; data curation, M.D.; writing—original

draft preparation, E.P.; writing—review and editing, M.I. and S.M.; visualization, E.P. and S.M.; supervision, M.I. All authors have read and agreed to the published version of the manuscript.

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