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Can interspecific competition explain the absence of saline species in freshwaters? A test using water beetles

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Abstract

The habitats a species occupies are not determined solely by its environmental tolerance, because biotic interactions can further restrict its realised niche. This mismatch between fundamental and realised niches is well documented in saline-associated aquatic insects, many of which tolerate freshwater conditions in the laboratory yet are largely confined to saline waters in nature. We tested whether interspecific competition could contribute to the absence of the halophilic diving beetle *Nebrioporus baeticus* in freshwater. We compared its response to restricted food availability with that of the freshwater-associated *N. clarkii* under freshwater conditions, using single- and mixed-species treatments. Survival was monitored over a 30-day period, while feeding behaviour was assessed on days 1 and 7 based on feeding time and the number of contacts with the food resource. Contrary to our expectations, the halophilic beetle was not competitively disadvantaged by the freshwater congener. Interspecific coexistence instead had a transient negative effect on the feeding behaviour of the freshwater species, but not of the halophilic species. These findings suggest that competition alone cannot explain the absence of halophilic species from freshwater habitats, indicating that other factors are likely involved (e.g., predation pressure, parasitism, or other biotic interactions).

Introduction

Understanding how species respond to environmental stress is a central question in ecology (Rapport & Whitford, 1999) and is essential for predicting how species and communities will respond to global environmental change (Lawlor et al., 2024). Species may persist under stressful conditions through physiological and ecological adaptations that allow them to tolerate a broad range of environmental conditions (ecological generalisation), or through adaptations that increase performance under a narrower range of conditions (ecological specialisation). However, the distribution of a species in nature does not necessarily reflect the full range of environmental conditions under which it can survive or maintain positive fitness (Carscadden et al., 2020). This distinction is captured by the concepts of the fundamental and realised niches: the fundamental niche encompasses the environmental conditions under which a species can persist in the absence of limiting biotic interactions, whereas the realised niche reflects the subset of those conditions occupied in nature after accounting for interactions with other organisms and other ecological and historical constraints (Hutchinson, 1957). Thus, a species may have a broad fundamental niche while occupying a relatively narrow realised niche.

The freshwater–saline continuum provides a particularly suitable system for investigating the mechanisms underlying this discrepancy (Reid et al., 2019). Salinity is a major environmental filter in inland aquatic ecosystems and strongly influences species distributions and community composition (Gasith & Resh, 1999; Millán et al., 2011; Gutiérrez-Cánovas et al., 2015). Aquatic insect communities show marked species turnover along salinity gradients, with many species occurring predominantly or exclusively at particular points along the gradient (Piscart et al., 2006; Gutiérrez-Cánovas et al., 2013; 2018). This pattern has traditionally been interpreted as evidence of ecological specialisation to saline conditions. However, physiological studies have revealed an apparent mismatch between the realised

and fundamental niches of many aquatic insects associated with saline waters (Arribas et al., 2019). Species considered halophilic (i.e., restricted to saline waters) based on their distribution can often survive and maintain osmotic balance not only in saline, hyperosmotic waters but also in freshwater or low-salinity conditions (i.e., hypoosmotic media) under laboratory conditions. Thus, they are physiologically euryosmoregulatory despite their apparently restricted distribution (Céspedes et al., 2013; Pallarés et al., 2015). Indeed, saline-associated insects may perform similarly to, or even better than, closely related freshwater species under low-salinity conditions in the laboratory, suggesting that physiological intolerance alone cannot fully explain their absence from freshwater habitats (Arribas et al., 2019).

This discrepancy raises a fundamental ecological question: if saline-associated species are physiologically capable of surviving in freshwater, why are they generally absent from these habitats in nature? As stated above, one possibility is that their freshwater distribution is constrained by biotic interactions with competitors, predators, pathogens and other organisms. In this context, the resident community may generate biotic resistance that prevents species from establishing in otherwise physiologically suitable habitats (Going et al., 2009; Rius et al., 2014). Interspecific competition is particularly relevant because it can influence resource acquisition, coexistence and community composition in aquatic ecosystems (Holomuzki et al., 2010). Therefore, differences in competitive ability between freshwater and saline-associated species could contribute to the restriction of the latter to saline habitats.

The intensity and outcome of competition may differ substantially between freshwater and saline ecosystems. Freshwater communities are typically taxonomically and functionally diverse, and species may exhibit considerable overlap in resource use, potentially increasing competition when resources are limited (Holomuzki et al., 2010). In contrast, saline inland waters often support less diverse communities dominated by a relatively small number of well adapted species (Millán et al., 2011), potentially reducing interspecific competitive interactions. Salinity itself can also modify the outcome of interactions between species, meaning that environmental stress may influence competitive relationships rather than simply acting as an independent environmental filter (Loureiro et al., 2013; Venâncio et al., 2017). This may reflect trade-offs between stress tolerance and competitive ability, both energetically costly processes, whereby adaptations to stressful environments comes at the expense of performance in less stressful environments (Scudder, 1983; Herbst, 2001). For example, Venâncio et al. (2017) found that relatively small increases in salinity shifted the competitive advantage between two algal species, while Qi et al. (2018) reported that stress-tolerant plant species had a lower competitive advantage under less stressful conditions.

Two possible non-mutually exclusive hypothesis could therefore explain the absence of saline-associated species in freshwaters. First, saline species may have lower competitive ability than freshwater species, particularly under freshwater conditions where the physiological adaptations to high salinity no longer provide an advantage. Second, their absence in freshwaters may persist even in the absence of a competitive disadvantage, if other physiological or ecological factors make saline habitats

more favourable overall, reflecting a balance between the costs and benefits of occupying alternative habitats. Understanding how environmental stress shapes realised niches and species coexistence is particularly relevant in the context of global changes in salinity regimes. Changes in salinity, including the salinisation of freshwaters and the dilution of naturally saline ecosystems, can alter aquatic biodiversity and community structure through both direct physiological effects and changes in species interactions (Cañedo-Argüelles et al., 2013, 2018; Cunillera-Montcusí et al., 2022). Salinity change may therefore influence not only which species can persist, but also the ecological interactions among the species that remain, potentially modifying patterns of coexistence and community structure.

Here, we tested whether interspecific competition for food could explain why a halophilic aquatic beetle, despite its broad physiological tolerance to freshwater conditions, is restricted to saline waters in nature. We used two closely related dytiscid beetle species with contrasting habitat preferences: the halophilic *Nebrioporus baeticus* (Schaum, 1864), which occurs in hypo- and mesosaline waters but has an efficient osmoregulatory capacity across a broad salinity gradient, and the freshwater-associated *Nebrioporus clarkii* (Wollaston, 1862), which has more restricted osmoregulatory capacity, being unable to survive under hyperosmotic conditions (Pallarés et al., 2015). Both species are predatory diving beetles with similar trophic niches, providing a suitable model to investigate whether biotic interactions may constrain the freshwater occurrence of the halophilic species.

We compared survival and feeding behaviour between these species under single and mixed-species below restricted food in freshwater. If the halophilic species, *N. baeticus*, is competitively disadvantaged in freshwater, its performance should decrease more strongly in the presence of its freshwater congener, *N. clarkii*, than under single-species conditions, resulting in reduced survival and/or feeding activity. Conversely, if the response of *N. baeticus* to interspecific coexistence is similar to or stronger than that of *N. clarkii*, this would suggest that competitive disadvantage alone is unlikely to explain its absence in freshwater.

Methodology

Study species and sampling

The genus *Nebrioporus* (family Dytiscidae) includes species occupying contrasting positions along the salinity gradient, making it a suitable model for investigating the role of biotic interactions in shaping habitat distributions. We selected two closely related *Nebrioporus* species with contrasting habitat preferences: *N. clarkii*, characteristic of continental subsaline to freshwater environments (conductivity range: 0.1–9 mS cm^{-1}; Pallarés et al., 2015), and *N. baeticus*, associated mainly with mesosaline environments (conductivity range: 4–160 mS cm^{-1}; Pallarés et al., 2015). Despite their phylogenetic proximity, the two species differ markedly in their habitat preferences and osmoregulatory capacities (Pallarés et al., 2015). Both species occur among gravel substrates in lotic environments and are predatory diving beetles with similar trophic niches (Toledo, 2009; Millán et al., 2014). *N. clarkii* is found mainly in lotic environments with moderate currents, such as headwater streams, middle reaches and

small rivers, whilst *N. baeticus* is more commonly associated with lower reaches of streams with high organic matter load, abundant cyanobacterial and diatom biofilms and sparse riparian vegetation (Millán et al., 2006; Millán et al., 2014).

Adult beetles were collected in November 2025 from two streams in south-eastern Spain: 75 individuals of *N. clarkii* were collected from Corneros stream (37°43'02.3"N, 1°54'19.1"W), and 75 of *N. baeticus* from Chícamo stream (38°12'58.3"N, 1°03'12.2"W). The salinity of each site, measured *in situ* using a conductivity-meter, was 0.8 and 7 gL^{-1}, for Corneros and Chícamo, respectively. Specimens were transported to the laboratory in ventilated containers placed inside a cool box to minimise temperature fluctuations during transport.

Upon arrival, individuals of each species were maintained separately in aquaria containing water from their respective collection sites and were not fed for two days to standardise their nutritional state before the experiment.

Experimental design

To test whether interspecific interactions affect the performance of the two species under freshwater conditions, individuals were randomly assigned to either single-species or mixed-species treatments. In the single-species treatment, 10 individuals of the same species were maintained together in each aquarium. In the mixed-species treatment, 5 individuals of each species were maintained together in the same aquarium, resulting in the same total density of 10 beetles per aquarium in both treatments.

Five independent aquaria were used for each species × treatment combination, resulting in 15 experimental aquaria in total. Each aquarium had a capacity of 1.2 L and contained 500 mL of commercial natural mineral water, together with a stone and a piece of mesh that provided resting surfaces and allowed the beetles to avoid continuous swimming and associated exhaustion.

Aquaria were continuously oxygenated using a capillary tube connected to an Air Professional aerator (360 L h^{-1}; Prodac, Italy). All aquaria were maintained at a controlled room temperature of 24 ± 1°C under natural light cycle.

Survival assessment

Aquaria were inspected daily throughout a 30-day experimental period to record mortality. To maintain a constant ratio of individuals to water volume throughout the experiment, the experimental volume was reduced by 50 mL for each dead individual. Thus, the initial density of 50 mL/individual was maintained throughout the experiment. Survival at the end of the experiment was expressed as the proportion of individuals alive on day 30 in each aquarium.

Feeding conditions and behavioural observations

Food availability was deliberately restricted to create conditions under which competition for food resources could occur. As chironomid larvae are recognised as an important food resource for predatory diving beetles (Carbonell et al., 2025), beetles were fed frozen chironomid larvae at a rate of one larva per five beetles per day.

Because the small size of the larvae and variation in their water content made individual weighing impractical, food quantity was standardised by larval length. Larvae of approximately 10 mm in length were used throughout the experiment. Thus, each aquarium received two 10-mm larvae per day, corresponding to approximately 2 mm of larval length available per individual beetle per day. Similarly, for every individual that died, 2 mm of larval length was removed.

Behavioural responses during feeding were recorded on days 1 and 7 of the experiment. Immediately after food was provided, two-minute video recordings were obtained using a Realme GT Master Edition mobile phone (Realme, China), positioned above the aquaria. The camera field of view included the entire water surface and perimeter of each aquarium, allowing all visible feeding activity to be recorded.

Because individual beetles could not be reliably distinguished and tracked throughout the recordings, behavioural variables were quantified at the species level within each aquarium rather than for individual beetles. The videos were visually analysed to record two variables for each species: (i) mean feeding time per individual (feeding time hereafter), calculated as the cumulative time spent feeding by all individuals of that species during the two-minute observation period and divided by the number of individuals of that species in the aquarium and (ii) the mean number of contacts with the food resource per individual (number of contacts hereafter), calculated as the total number of contacts made by all individuals of each species and divided by the number of individuals of that species in the aquarium.

Data analyses

All statistical analyses were carried out in R v.4.5.2. (R Core Team, 2025). The effect of interspecific competition treatment, species and their interaction on long-term survival and feeding behaviour responses was assessed. The survival of individuals on day 30 of the experiment, expressed as a proportion (0–1), was assessed using a generalised linear model (GLM) with a binomial error distribution and a logit link function. The model was checked for overdispersion.

To explore the effect of interspecific competition on behavioural resource acquisition responses, the feeding time (in seconds) and the number of contacts with the food resource were analysed. These variables were analysed independently at two time points, corresponding to the two recording periods: day 1 and day 7. A zero-inflated negative binomial (ZINB) model was fitted for feeding time, due to the observed overdispersion and the presence of zero observations associated with individuals that did not

feed during the observation period. The number of contacts of each species with the chironomid larvae was assessed using a GLM with a Gaussian error distribution and identity link function.

Where significant effects were detected, post hoc comparisons were carried out based on estimated marginal means using Tukey's correction. A significance level of $\alpha = 0.05$ was used in all analyses. In all analyses, the aquarium was considered the experimental unit (i.e. replicate).

Results

Effects of interspecific competition on survival

Survival after 30 days did not differ significantly between species, experimental treatments, or their interaction (Table 1). Under single-species conditions, both species showed similar relatively high survival rates (Fig. 1). Under mixed-species conditions, survival was slightly lower in *N. clarkii* than in *N. baeticus*, but this difference was not statistically significant. Mean survival was ≥ 63% in all treatments.

Table 1
Effect of species, experimental treatment (single- vs mixed-species conditions), and their interaction on survival at the end of the 30-day experimental period.

Factor	d.f.	Deviance	Residual d.f.	Residual Deviance	*P*-value
Species	1	2.660	18	20.819	0.103
Treatment	1	0.109	17	20.711	0.741
Species x Treatment	1	1.980	16	18.730	0.159
d.f.: degrees of freedom					

Effects of interspecific competition on feeding time

At the beginning of the experiment (day 1), feeding time differed significantly between species, and the treatment alone and the species × treatment interaction were also significant (Table 2). Post hoc comparisons revealed that the effect of competition was different for each species. In *N. clarkii*, feeding time was significantly lower under mixed-species conditions than under single-species conditions, whereas no significant difference between treatments was detected in *N. baeticus*. Comparisons between species within each treatment showed that, under mixed-species conditions, *N. baeticus* had significantly higher feeding times than *N. clarkii*, while, under single-species conditions, there were no significant differences between species (Fig. 2).

Table 2
Effect of species, experimental treatment (single- vs mixed-species conditions), and their interaction on feeding time (s) at the beginning of the experiment (day 1) and after 7 days.

Factor	χ^2	d.f.	*P*-value
Day 1			
Species	45.208	1	< 0.001
Treatment	4.708	1	0.0300
Species x Treatment	29.841	1	< 0.001
Day 7			
Species	3.790	1	0.052
Treatment	2.230	1	0.135
Species x Treatment	0.721	1	0.396
d.f.: degrees of freedom			

At the end of the experiment (day 7), feeding time did not differ significantly between species, between treatments, or for the species × treatment interaction (Table 2). Although there were no significant differences, like on day 1, *N. baeticus* continued to have a higher feeding time than *N. clarkii* in all treatments (Fig. 2).

Effects of interspecific competition on feeding contacts

At the beginning of the experiment (day 1), only the species × treatment interaction had significant effects on the number of contacts with the food resource, whereas the effect of species and treatment alone were not significant (Table 3). Post hoc comparisons revealed that significant differences between species were only found within the mixed-species condition, where *N. baeticus* made significantly more contacts with the food resource than *N. clarkii* (Fig. 3).

Table 3
Effect of species, experimental treatment (single- vs mixed-species conditions), and their interaction on the number of contacts with the food resource at the beginning of the experiment (day 1) and after 7 days.

Factor	F	d.f.	*P*-value
Day 1			
Species	3.101	1	0.097
Treatment	2.642	1	0.124
Species x Treatment	5.303	1	0.035
Day 7			
Species	2.722	1	0.119
Treatment	0.747	1	0.400
Species x Treatment	2.228	1	0.155
d.f.: degrees of freedom			

After one week (day 7), no significant effects were detected for any of the factors studied (Table 3).

Discussion

Our study tested whether interspecific competition for food could contribute to the absence of the halophilic species *N. baeticus* in freshwater. We predicted that coexistence would have stronger negative effects on the halophilic species than on its freshwater congener *N. clarkii*, or alternatively a similar or weaker effect. Contrary to these predictions, coexistence did not reduce the survival or feeding activity of the halophilic species under the conditions tested. Instead, the clearest effects of coexistence were behavioural changes in *N. clarkii*.

Interspecific coexistence affects feeding behaviour but not survival

Against our prediction, interspecific coexistence initially reduced the feeding time and number of contacts with the food resource in the freshwater species *N. clarkii*, whereas the halophilic *N. baeticus* maintained similar feeding activity across treatments. The differences observed for the behavioural response variables were no longer detectable after one week, and neither species showed detectable differences in survival over the 30-day experiment. Thus, coexistence produced an immediate but apparently transient and asymmetric behavioural response, without detectable survival consequences during the experimental period.

These results contrast with the hypothesis that *N. baeticus* has lower competitive ability in freshwater because of the energetic costs associated with adaptations to saline conditions (Scudder, 1983; Herbst, 2001; Qi et al., 2018). Instead, *N. baeticus* maintained, and in the mixed treatment exceeded, the feeding activity of *N. clarkii* at the beginning of the experiment. Although feeding behaviour alone does not demonstrate competitive superiority, these results indicate that *N. baeticus* was not competitively disadvantaged under the conditions tested and may have exerted a negative effect on the resource-use behaviour of *N. clarkii*. However, the absence of a detectable feeding disadvantage in *N. baeticus* does not rule out physiological costs of salinity adaptation that may affect other aspects of performance or become apparent under different conditions.

Our results suggest that physiological tolerance to salinity and competitive ability are not necessarily negatively associated. Although adaptations to saline conditions may entail energetic costs, these do not appear to limit resource acquisition capacity in freshwater in *N. baeticus*. Indeed, its broad osmoregulatory capacity allows it to maintain physiological function across a wide salinity gradient (Pallarés et al., 2015), and its tolerance to other environmental stressors may further contribute to its ecological flexibility (Sánchez-Fernández et al., 2010; Céspedes et al., 2013).

Behavioural responses may precede demographic consequences

The transient feeding behavioural response of *N. clarkii* suggests that interspecific interactions may initially alter resource-use behaviour without necessarily producing immediate demographic effects. This temporal pattern could reflect behavioural adjustment or habituation to the presence of the other species, although our experiment was not designed to distinguish among these mechanisms.

The decoupling between behaviour and survival is ecologically relevant. Feeding behaviour can respond rapidly to the presence of a competitor, potentially reflecting short-term changes in perceived competition or resource accessibility before these interactions translate into measurable effects on survival. Alternatively, the initial response may have been too small or too short-lived to produce cumulative energetic costs that affected survival. This highlights the importance of considering the temporal dynamics of behavioural interactions when assessing competition, as short-term changes in resource use may represent an early response to coexistence that is not necessarily reflected in conventional demographic measures such as survival.

Competition alone is unlikely to explain the absence of N. baeticus in freshwater

If the absence of *N. baeticus* in freshwater is not explained by physiological intolerance or a reduced ability to compete with freshwater species, why is it predominantly found in saline habitats? One possibility is that the benefits of exploiting environments with lower interspecific competitive pressure outweigh the physiological costs associated with salinity tolerance (Pallarés et al., 2015; Arribas et al., 2019). From this perspective, *N. baeticus* may be an effective competitor in freshwater too, but its

occurrence in these environments could be constrained by the combined costs of competition and other biotic and abiotic stressors absent in saline waters. For example, although this species is adapted to mesosaline conditions, maintaining osmotic balance in freshwater may also impose physiological costs (Rivera-Ingraham & Lignot, 2017), as the mechanisms required for ion and water regulation differ between hypo and hyperosmotic environments. Beyond competition, other biotic interactions may play a significant role in the distribution of both species (Holomuzki et al., 2010). Parasites (Hatcher et al., 2006; Hasik et al., 2023), symbiotic microorganisms or predators could significantly affect the performance of individuals and alter the outcome of competitive interactions. In fact, saline environments tend to harbour less diverse communities and experience lower predation pressure than freshwater systems (Millán et al., 2011). The association of *N. baeticus* with saline habitats may therefore reflect a balance between physiological costs and the benefits of experiencing fewer or different biotic interactions, rather than differences in physiological tolerance or competitive ability alone.

These mechanisms shaping the distribution of aquatic invertebrates across salinity gradients are particularly relevant under global change. Freshwater salinisation is a widespread global environmental problem driven by human activities and amplified by climate change, whereas naturally saline inland waters can also experience anthropogenic dulcification, particularly through freshwater inputs associated with irrigated agriculture in arid and semi-arid regions (Gutiérrez-Cánovas et al., 2018; Cunillera-Montcusí et al., 2022). These processes are relevant in Southeast Spain, where both *N. clarkii* and *N. baeticus* occur and human activities have altered the salinity of inland waters (e.g., Velasco et al., 2006; Gutiérrez-Cánovas et al., 2009). These changes may modify the environmental filters that currently structure the distributions of freshwater and halophilic species, potentially increasing opportunities for contact and modifying their distribution patterns under future global change scenarios.

Limitations and future perspectives

Experimental studies of competition in aquatic insects remain scarce, making our study a valuable contribution to understanding whether interspecific competition can help explain the absence of halophilic species in freshwater environments. Nevertheless, several limitations should be considered when interpreting the results.

First, although food availability was deliberately restricted to promote competition, we cannot exclude the possibility that the resource limitation was insufficient to produce stronger or more persistent effects. Likewise, the 30-day experimental period may have been too short to detect demographic consequences. Moreover, survival is a relatively conservative measure of competitive effects and may not capture earlier physiological or energetic costs (Sokolova et al., 2012). Additional variables, such as body mass, energy reserves, physiological stress markers, growth or reproduction, could reveal sublethal effects that are not immediately reflected in mortality and provide a more sensitive assessment of the costs of competition.

Second, our experiment considered competition for a single food resource, whereas natural populations may compete simultaneously for multiple resources, including food, shelters, resting areas, breeding sites or suitable oviposition sites (Hart, 1987; Holomuzki et al., 2010). Because the strength and direction of competition may vary depending on the resource involved (Holomuzki et al., 2010), the interactions observed in this experiment may not fully represent those occurring in natural populations. Moreover, competitive interactions may differ across life stages. Larval or juvenile stages may exhibit different sensitivities to competition, and competitive effects experienced during these stages may carry over into adulthood, producing demographic consequences that remain undetected when only adults are studied (Hanly & Haase, 2016; Noden et al., 2016). Future studies should therefore evaluate competition across multiple resources and life stages, ideally incorporating, where possible, multiple generations. Competition should also be investigated under different levels of resource limitation and, as suggested by Rius et al. (2014), in the presence of other potential mechanisms of biotic resistance such as predation, which would provide a more realistic assessment of the factors shaping coexistence.

The ability to detect competitive effects may also have been constrained by the sample size and the high degree of inter-individual variability. Differences in age, sex, prior physiological condition or environmental history may contribute to variation in the response to competition. Future experiments with a larger number of replicates and greater control of these sources of variability would therefore improve the assessment of the magnitude and consistency of competitive interactions between the two species.

Conclusion

More broadly, our findings highlight that species distributions cannot always be predicted from physiological tolerance or competitive interactions considered in isolation. Understanding the realised niches of aquatic invertebrates requires an integrated approach that considers physiological constraints, multiple biotic interactions, and their variation across environmental conditions and life stages. This is particularly relevant for the conservation of inland aquatic ecosystems, where freshwater salinisation and the dilution of naturally saline habitats may alter both environmental filters and species interactions. Identifying the mechanisms underlying species distributions is therefore essential to anticipate community responses to changing salinity regimes and to develop effective conservation strategies for aquatic biodiversity.

Declarations

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Competing interests

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

Authors' contribution

SM-T, SP, JV and DS-F conceived and designed the study. SM-T, SP, JV and EMM-H conducted the experiments and collected the data. SM-T and SP analysed the data. SM-T, SP, JV, EMM-H and DS-F drafted the manuscript. All authors contributed to the interpretation of the results, critically revised the manuscript, and approved the final version.

Data availability statement

The data supporting the findings of this study will be deposited in a public repository and made available upon publication of the article.

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Figures

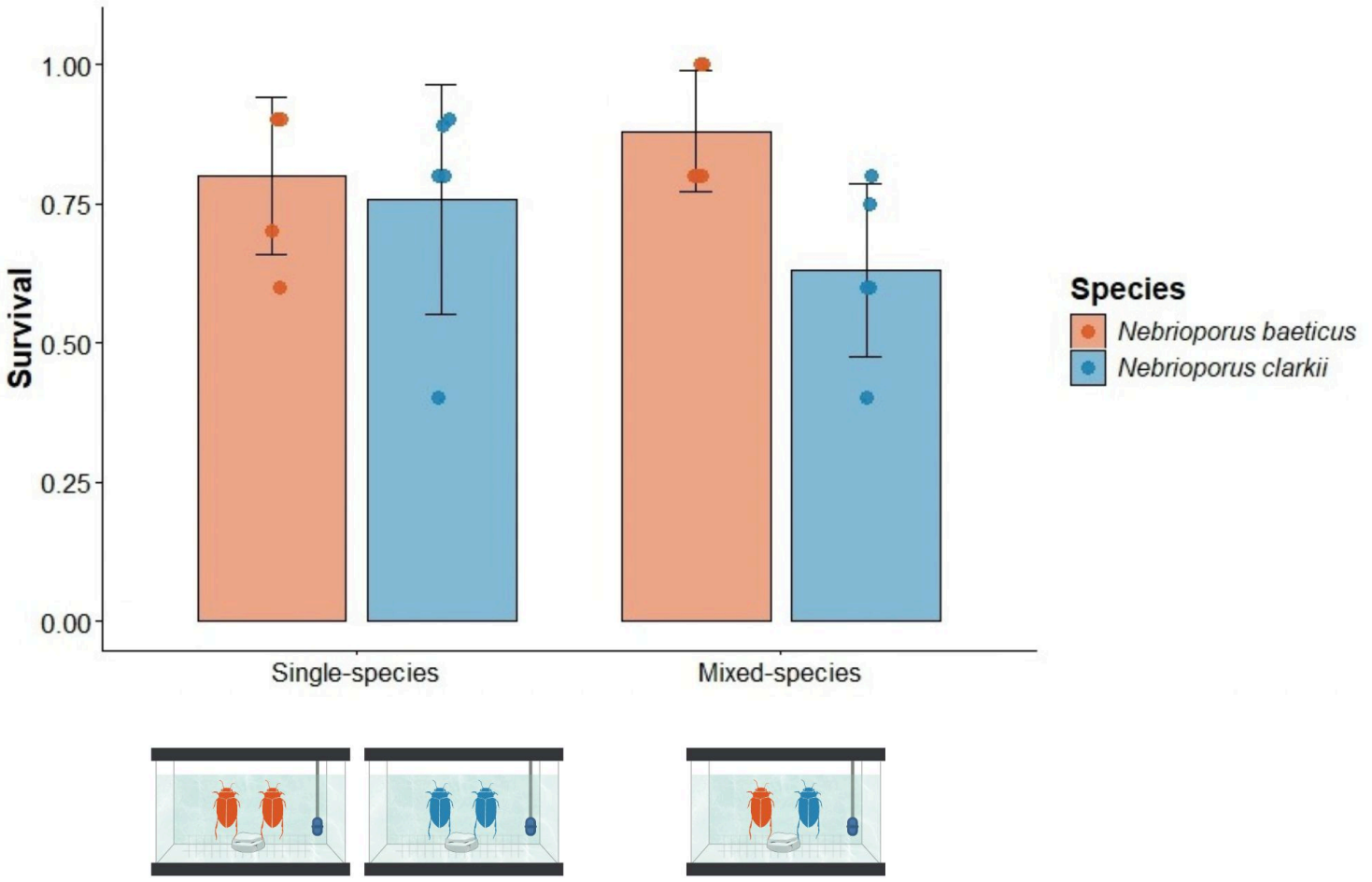


Figure 1

Survival proportion (0–1) of *Nebrioporus baeticus* and *N. clarkii* after 30 days under single- and mixed-species conditions. Bars represent mean survival ± SE, and dots represent individual experimental replicates

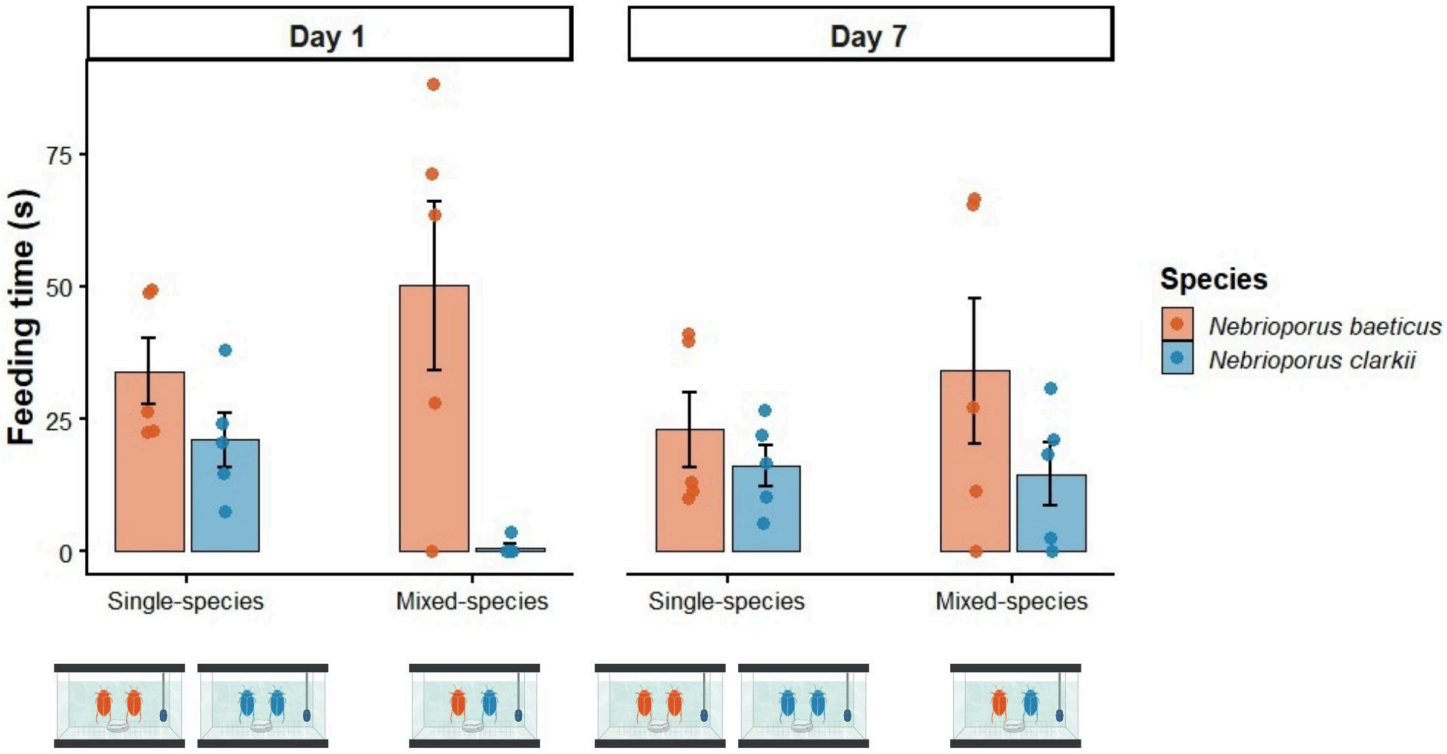


Figure 2

Feeding time (s) of *Nebrioporus baeticus* and *N. clarkii* at the beginning of the experiment (day 1) and after 7 days under single- and mixed-species conditions. Bars represent mean feeding time ± SE, and dots represent individual experimental replicates

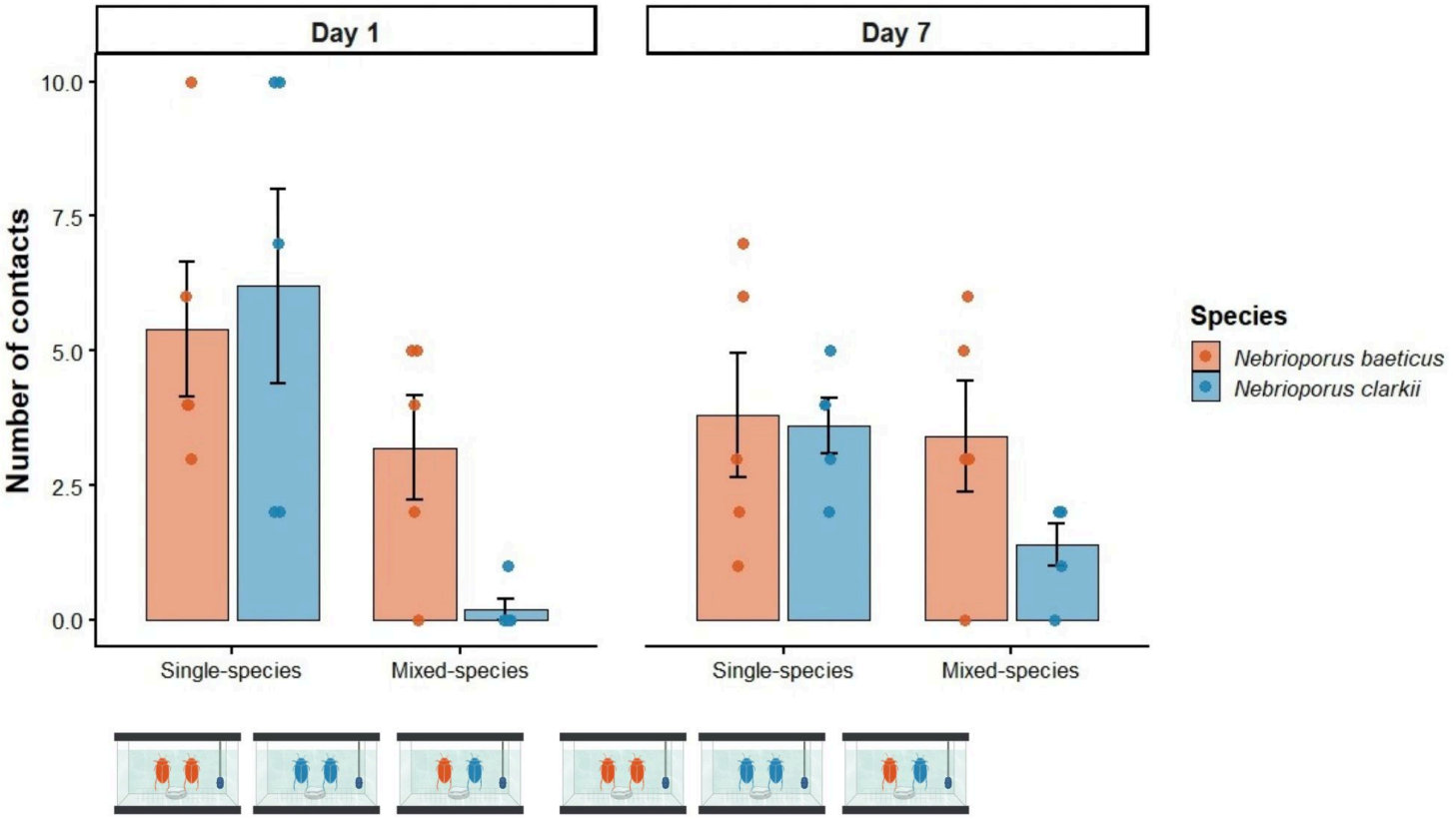


Figure 3

Number of contacts with the food resource made by *Nebrioporus baeticus* and *N. clarkii* at the beginning of the experiment (day 1) and after 7 days under single- and mixed-species conditions. Bars represent mean number of contacts ± SE, and dots represent individual experimental replicates