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„Abundance–suitability relationships in tropical Odonata“

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Abstract

Environmental niche models are becoming increasingly important to investigate the distribution of species in times of global change. These models are mostly based on occurrence rather than abundance data, but for many applications abundances are the more relevant parameter. As this data is rarely available, predicting abundances based on habitat suitability derived from occurrence models could help ameliorate this problem. A relationship between abundance and suitability appears to generally exist, but its predictive power is highly variable. In this study abundance–suitability relationships in tropical Odonata species were explored. Fine-scale environmental variables were used to model habitat suitability, which was then related to observed abundances. Additionally, it was tested if the species' degree of habitat specialisation determined the strength of these relationships. Abundance was significantly related to habitat suitability in ten of eleven Odonata species. Yet, the explanatory power of these relationships was only moderate for most species. The strength of these relationships was further significantly related to the species' degree of habitat specialisation. This suggests that occurrence models can be used to infer abundances. Caution is advised, however, as their predictive power is highly variable and can potentially be influenced by numerous factors. As demonstrated by the effect of the species' degree of habitat specialisation.

Keywords: Costa Rica, damselflies, dragonflies, environmental niche models, habitat specialisation, habitat suitability, Odonata, species abundance, tropics

For a German abstract see Appendix B
Für eine deutsche Zusammenfassung siehe Appendix B

Introduction

Patterns of species distribution and abundance have long intrigued biologists and studying the mechanisms responsible for these patterns is one of the key areas of ecological research (Brown, 1984). Understanding the underlying processes is especially important in the present time, with global change altering species' distributions (Guo et al., 2018; Hill et al., 2001) and increasing extinction rates (Ceballos et al., 2015).

Numerous statistical techniques, referred to as ecological niche models (ENMs) have been developed to investigate species distributions. These models relate species occurrence (presence-absence) or abundance data to environmental variables and predict probabilities of occurrences or the most probable abundances, respectively (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). The applications of such models are manifold, including the identification of priority areas for conservation, forecasting the invasion potential of species and predicting the effects of climate change (Peterson, 2006). As occurrence data is usually considerably easier to obtain than abundance data, ENMs have mostly been based on occurrence rather than abundance data (Kissling et al., 2018; Waldock et al., 2022). Yet, for many applications, e.g., assessing a species' extinction risk, modelling abundances may be more appropriate (Ashcroft et al., 2017; Ehrlén & Morris, 2015), as presence-absence models do not differentiate between small and large populations, albeit population size is a strong predictor for extinction risk (O'Grady et al., 2004). Assessing species' extinction risk based on occurrence data could therefore potentially lead to the conservation of marginal sink populations rather than the most viable core populations (Ashcroft et al., 2017).

Still, the issue remains that abundance data is rarely available to the necessary extent. Estimating abundances from presence-absence models, if possible, could ameliorate this problem. Following the concept of the Hutchinsonian niche (Hutchinson, 1957), Brown (1984) proposed that both a species' distribution and abundance depend on a number of different environmental variables. Population densities of a species should be highest in habitats most closely matching their ecological requirements. As the favourable environmental conditions in high-quality habitats relate to the successful survival and reproduction of a species (Morrison et al., 2006), habitat quality is frequently assessed by means of abundance (Johnson, 2007).

Occurrence probabilities derived from presence-absence models are regularly interpreted as environmental suitability scores (Peterson, 2006), which themselves are often assumed to be correlated with habitat quality (Gutiérrez et al., 2013). It may therefore be plausible to expect the suitability of a habitat for a particular species, as predicted by a model, to be related to the species' abundance in this habitat. This putative relationship is most commonly referred to as the abundance–suitability (AS) relationship.

During the last two decades, this AS relationship has received some attention and multiple studies have been conducted to provide evidence for its existence. These studies covered a variety of different taxonomic groups and while some did find strong support for a link between habitat suitability and abundance (e.g., de la Fuente et al., 2021; Gutiérrez et al., 2013; Oliver et al., 2012; Weber & Grelle, 2012), others reported no to only weak AS relationships (e.g., Dallas & Hastings, 2017; Filz et al., 2013; Jiménez-Valverde et al., 2009; Nielsen et al., 2005). Nonetheless, a recent meta-analysis concluded that suitability and abundance are generally positively correlated, and that presence-absence data can be a reasonable proxy for abundance (Weber et al., 2017). However, it was cautioned against accepting the AS relationship as universal, as multiple factors could be reasonably suspected to affect its strength.

In arthropods for example, abundances can fluctuate considerably across time, potentially weakening AS relationships (Jiménez-Valverde et al., 2009). This is highlighted by stronger correlations between habitat suitability and abundance in vertebrates compared to invertebrates, with the latter also exhibiting larger variations in reported correlation coefficients (Weber et al., 2017). Another influential characteristic of species may be their vagility, as more vagile species show a tendency towards stronger AS relationships compared to sedentary species (Jiménez-Valverde et al., 2009). Nielsen et al. (2005) further suggested that suitability and abundance should be more closely linked in specialist species. Finally, the choice of predictors used for modelling suitability could affect the resulting AS relationships (de la Fuente et al., 2021; Weber et al., 2017). Climatic variables are the most commonly utilised predictors for deriving habitat suitability, but correlations between suitability and abundance were higher in studies considering not only climatic and topographic, but also additional fine-scale environmental variables (Weber et al., 2017). Although the results of these studies suggest that a relationship generally exists between suitability and abundance, the strength of this relationship and thus the potential for predicting abundances from presence-absence data appears to be highly variable.

In this study we therefore aim to further explore AS relationships in tropical odonates (i.e., dragonflies and damselflies; Insecta: Odonata), at a relatively small spatial scale. The required abundance data was collected over multiple years at sampling sites spread across a highly variable landscape in Costa Rica. Suitability values for several different species were then derived from presence-absence models utilising environmental variables measured directly in the field. These model-derived suitability values were related to the abundances of the respective species and the strength of the resulting AS relationships to the species' degree of habitat specialisation.

Overall, this study is concerned with answering the following questions: (1) Do significant AS relationships exist in tropical odonates and if yes, are they strong enough to reasonably predict abundances? (2) Is the strength of a species' AS relationship related to its degree of habitat specialisation?

Based on the studies published so far, we expect significant and strong positive AS relationships in tropical Odonata. The fact that adult odonates are generally highly mobile species (Stevens & Bailowitz, 2009) should contribute to strong AS relationships (Jiménez-Valverde et al., 2009). As should the inclusion of fine-scale environmental variables for modelling suitability, since these variables may better represent local conditions and could thus be more relevant than climatic variables (de la Fuente et al., 2021; Weber et al., 2017). Based on suggestions made by other authors we would further expect specialist species to exhibit stronger AS relationships than generalist species (Jiménez-Valverde et al., 2009; Nielsen et al., 2005).

Methods

Study area

The study area is situated in the southern Pacific lowlands of Costa Rica, in the Puntarenas province. It comprises a large network of drainages, rivers and small tributaries (hereafter collectively referred to as rivers) that cross the Piedras Blancas National Park, the Golfito Forest Reserve and the adjacent agricultural areas surrounding the village La Gamba (8.70783, −83.18539; 65 m a.s.l.; Figure 1). The countryside consists of a wide variety of different land cover types, ranging from pristine primary forests, over secondary forests to cultivated land (i.e., pastures and oil palm plantations) and small settlements (Weissenhofer et al., 2008). The climate is characterised by high annual rainfalls (c. 5,800 mm) with rainfall maxima and minima occurring around October (c. 800 mm) and February (c. 200 mm), respectively (Weissenhofer & Huber, 2008).

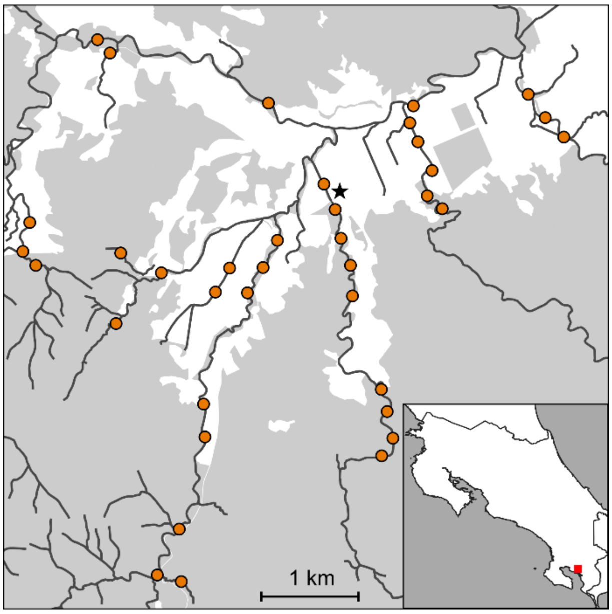

Figure 1. Overview of the study area surrounding the village La Gamba (black star) and indication of its position within Costa Rica (red square, bottom right). Forest areas are shaded in grey. Orange circles indicate Odonata sampling sites, and black lines represent rivers.

Odonata surveys

Data on Odonata abundances was collected over the course of three sampling periods at sites distributed along the rivers in the study area. The first two surveys were conducted from November 2015 to January 2016, and October 2016 to February 2017, respectively. For these surveys, sampling sites were chosen to represent one of four habitat types: forest interior, forest margin, gallery forest and open land. Eight sites, at least 200 m apart from each other, were established per habitat type, for a total of 32 sampling sites. Each of these sites was sampled a total of ten times during the two surveys (Sarah Degenhart and Felix Meyer, unpublished). A third survey was conducted between February and March 2018 which comprised six different sampling sites that were sampled three times each. The sites of this third survey were specifically chosen to represent habitat types not yet covered by the two previous surveys (e.g., drainages in oil palm plantations or very wide river sections).

All three surveys followed the same general sampling method. At each site, a 50-metre transect was established along the river stretch. Transects were surveyed between 8 am and 5 pm for one hour per visit and every encountered odonate was recorded. Individuals we could not identify in the field were killed with ethyl acetate and collected for later identification.

The nomenclature used in this study follows Paulson and Haber (2021).

Environmental variables

To characterise Odonata habitats, several environmental variables were recorded along the rivers (Table 1). However, as the initial concept for this study differed from the final approach presented here and required characterisation of the complete riverine system in the study area, these environmental variables were not just recorded for the 38 Odonata sampling sites mentioned above. Instead, all rivers were divided into sections of 200 m length, resulting in 233 such sections. At the centre points of these sections, 50-metre transects were established and environmental variables were recorded along these transects.

The following 9 environmental variables were recorded directly in the field to characterise each of the river sections. These variables were chosen as they can be assumed to potentially affect the occurrence of Odonata species. We quantified the amounts of both woody debris and rocks protruding above the water surface, the amount of surrounding vegetation hanging over the water surface, as well as the presence of mostly gravelled, but at least unvegetated riverbanks on an ordinal scale from missing (0) to very abundant along the whole transect (5). The average grain size of the stream bed sediments was also classified on an ordinal scale, ranging from very fine (1; mainly silt and sand) to very coarse (5; predominantly cobbles and boulders). The width of the river (m) was estimated at its widest point. However, as water levels can fluctuate greatly due to precipitation, or lack thereof, width was not estimated based on the current water level but rather the highest level it commonly reaches, as indicated by e.g., relatively recent depositions of fluvial sediments along the riverbanks. Flow velocity of the river (m/s) was measured using a chip log, a small board weighted by lead which is attached to a string. The chip log was dropped into the water at the centre of the river cross section and the time it required to travel 10 m (the length of the string) was then used to calculate the flow velocity. Further, the maximum height of the vegetation (m) at either side of the transect within a 5-metre buffer was estimated, as well as the canopy cover (%) directly above the waterbody in 10% increments.

Table 1. Environmental variables recorded to characterise individual river sections, including their units (if applicable), the scales on which the ordinal variables were measured, as well as mean, minimum and maximum values for the continuous variables.

Variable	
Ordinal variables	**Scale**
Protruding woody debris	0 – 5
Protruding rocks	0 – 5
Overhanging vegetation	0 – 5
Riverbank	0 – 5
Grain size of stream bed sediment	1 – 5
Continuous variables	**Mean (min. – max.)**
River width (m)	9.7 (1.0 – 28.0)
Flow velocity (m/s)	0.5 (0.1 – 1.7)
Height of surrounding vegetation (m)	15.0 (0.1 – 42.0)
Canopy cover (%)	26.6 (0.0 – 90.0)
Fraction of old growth forest in a 50-m buffer	0.3 (0.0 – 1.0)
Fraction of young secondary forest in a 50-m buffer	0.3 (0.0 – 1.0)
Fraction of oil palm plantations in a 50-m buffer	0.2 (0.0 – 1.0)
Fraction of open land in a 50-m buffer	0.2 (0.0 – 1.0)
Fraction of settlements in a 50-m buffer	0.02 (0.0 – 0.5)
Linearity of river section	0.9 (0.3 – 1.0)

An additional 6 environmental variables were measured using the GIS software QGIS (QGIS.ORG, 2019). First, a map of the different habitat types in the study area was created, based on the vegetation map published by Weissenhofer et al. (2008), the most recent aerial photographs (Google Earth Pro, 2015) and information obtained directly in the field. Five different habitat types were differentiated: old growth forest (i.e., primary and old secondary forests), young secondary forest, oil palm plantation, open land, and settlement (including gardens). Then, for each of the river sections, the fraction of the area covered by the individual habitat types in a 50-metre buffer around the river section was calculated. To prevent buffers of adjacent river sections from overlapping, the buffers were created around the central 100 m stretch of the individual river sections. Finally, the linearity of the individual river sections was quantified by dividing the distance between the two endpoints of the river section by the total length of the section (i.e., 200 m in most cases). This results in a linearity value of 1 for a completely straight section, and a much lower value for e.g., S-shaped sections.

The biological relevance of these variables can be inferred for a variety of reasons. Some (e.g., woody debris, overhanging vegetation) may represent potential perching structures, while others (e.g., flow velocity, stream bed sediment) may indicate larval habitat quality (Corbet, 2004). The habitat buffers could describe the different foraging habitats available to adults at a specific site, and the linearity value of a river section may allow for some inference regarding habitat heterogeneity. However, individual variables can be important for different aspects of odonate life histories. For example, the mentioned perching structures may also be used for oviposition by some species.

Habitat specialisation

To quantify the species' degree of habitat specialisation, a principal component analysis (PCA) based on the environmental variables of all 233 surveyed river sections was calculated in advance. As the environmental variables included both ordinal and continuous variables, the PCA was calculated using the 'mixedCor' and 'principal' functions in the 'psych' package (Revelle, 2021) which can handle this kind of mixed data. Subsequently, the number of principal components to be retained was determined using the Kaiser-Guttman criterion (only components with eigenvalues > 1; Guttman, 1954; Kaiser & Dickman, 1959). Then, for each species, the principal component scores of all sampled sites it occurred in were extracted. These scores were used to calculate the species' habitat niche breadth by constructing hypervolumes via one-class support vector machine learning models using the 'hypervolume' function in the 'hypervolume' package (Blonder et al., 2014). To make this measure more easily interpretable as the degree of habitat specialisation, the initial hypervolumes were normalised and inverted, so that the resulting values ranged from 0 (highly unspecialised) to 1 (highly specialised).

Suitability models

Habitat suitability values for the different Odonata sampling sites were calculated separately for each species using logistic regressions, relating species' occurrences (presence-absence) to the environmental variables. For this purpose, abundance data were converted to occurrence data, only distinguishing between absences and presences of a given species at the individual sites. To mitigate the risk of single stray individuals observed during a survey potentially obscuring true absences, a species was also defined as absent from a site when it was encountered there only once across all replicate samples (i.e., singletons were removed).

At one site sampled in the first two surveys, the waterbody had dried out by the time the environmental variables of the river sections were recorded. This site was therefore excluded, reducing the number of Odonata sampling sites considered for further analyses to 37.

Continuous predictor variables (i.e., river width, flow velocity, vegetation height, canopy cover, the five habitat type buffers and linearity of the river section) were square-root transformed and further standardised to zero mean and unit standard deviation. Before calculating the models, the correlation structure of all predictor variables was checked to avoid high collinearity ($r/\rho \geq 0.7$ or ≤ -0.7). When predictors were highly correlated, the one predictor that was on average most highly correlated with the remaining predictors was excluded from all further analyses.

To avoid problems with model fit, only species with a sufficient number of both presences and absences were included in the analyses. Hence, the set of model species only comprised species which were present at a minimum of 10 (> 25% of all sampled sites), and a maximum of 27 sites (< 75% of all sampled sites).

For these model species, logistic regression models were calculated including either one or two predictor variables. All possible combinations of predictor variables were considered, and for every predictor both linear and quadratic terms were included. As the number of predictors per model had to be limited due to sample size, an information-theoretic approach using multimodel inference was applied to derive habitat suitability values not based on only a single model but a larger set of the models ('confidence set'; Burnham & Anderson, 2002, 2004). This approach can mitigate model selection bias, thus leading to more accurately estimated suitability values. To obtain this confidence set, we first calculated the Akaike information criterion adjusted for small sample size (AIC_C; Hurvich & Tsai, 1989) for every model and then calculated their corresponding Akaike weights (Burnham & Anderson, 2002). These weights were summed from largest to smallest until their sum reached 0.95. The corresponding models then made up the 95% confidence set. The parameter estimates of the models in this set were averaged and weighted by their associated Akaike weights. If a certain variable was not in a given model its parameter estimate was set to 0, to not bias its averaged parameter estimate away from zero (Burnham & Anderson, 2002). Suitability for a given species at each of the sampling sites was then derived based on these averaged parameter estimates. The calculation of AIC_C values and Akaike weights, as well as model averaging were performed using the 'MuMIn' package (Bartoń, 2022).

Abundance–suitability relationships

To evaluate AS relationships, observed abundances were regressed against habitat suitability, separately for each species using ordinary least squares (OLS) regressions. For this purpose, the relative mean abundances were calculated by first averaging the abundances across all replicate samples for each site and then dividing these mean abundances by the maximum mean abundance. These relative mean abundances were then log transformed. To avoid the problem of taking logarithms of zero, abundances were log (x + 1) transformed. To address the potentially non-linear nature of AS relationships, the OLS regressions included a quadratic term for the effect of suitability on abundance.

As some authors (e.g., Pearce & Ferrier, 2001) have shown that the predictive performance of AS relationships can be substantially worse when removing sites at which a species was absent, we evaluated AS relationships twice for each species. For the first approach, we simply considered all observed abundances for a species, which also included absences (i.e., abundances = 0) and related them to the corresponding suitability values. In the second approach we discarded absences, thus only relating abundances-when-present to suitability.

Correlations have shown to be high, while the predictive power often remains relatively weak (e.g., VanDerWal et al., 2009). Therefore, we used the R^2, i.e., the explanatory power of the OLS regressions, which should be a more representative measure, to quantify the strength of AS relationships. However, as these relationships are often measured by means of correlation coefficients, we also calculated Spearman’s rank correlation coefficient (ρ) to ease comparability.

Effects of habitat specialisation

The strength (i.e., R^2) of the AS relationships considering all abundances (i.e., including absences) was then regressed against the respective species’ degree of habitat specialisation via OLS regression. This regression included only a linear term for the effect of habitat specialisation on the strength of the AS relationship.

All analyses were performed using R (R Core Team, 2021) and plots were created using the ‘ggplot2’ package (Wickham, 2016).

Results

Across all three survey periods a total of 4532 Odonata individuals belonging to 62 species and ten families were recorded. After removing singletons, eleven of these species fulfilled the predetermined criterion of occupying between 10 and 27 sites (Appendix Table A1), thus allowing them to be considered for the suitability models.

Two of the environmental variables, vegetation height and canopy cover, emerged as highly correlated (r = 0.73; Appendix Table A2). Of the two variables, canopy cover on average exhibited stronger correlations with the other predictor variables and was therefore excluded from all further analyses, reducing the number of predictors to 14.

Habitat specialisation

The first five principal components of the PCA calculated to derive the species’ degree of habitat specialisation had associated eigenvalues > 1. These five principal components explained a combined 69% of the variance (for more detailed information, including principal component loadings see Appendix Table A3). The species' degree of habitat specialisation (Table 2) derived from hypervolumes calculated using the scores of occupied sites along these five principal components was moderately, but not significantly, correlated with the number of sites the species occupied ($\rho = 0.57$, $p = 0.068$).

Table 2. Degree of habitat specialisation for the eleven model species, derived from normalising and inversing the hypervolumes which were calculated based on the scores of the first five principal components at sites occupied by the respective species.

Species	**Hypervolume**	**Degree of habitat specialisation**
Argia cupraurea	4.93	0.52
Argia oculata	2.91	0.76
Argia oenea	1.13	0.98
Argia pulla	9.20	0.00
Dythemis sterilis	5.79	0.41
Enallagma novaehispaniae	1.39	0.94
Erythrodiplax fusca	4.02	0.63
Hetaerina caja	5.54	0.44
Hetaerina fuscoguttata	0.93	1.00
Hetaerina titia	2.38	0.82
Heteragrion erythrogastrum	2.45	0.82

Suitability models

A total of 105 logistic regression models (14 single- and 91 two-predictor models) were calculated for each of the eleven model species. The 95% confidence sets, from which suitability values for these species were derived, comprised between 3 and 39 of the 105 possible models and included between 5 and 14 different predictors (Appendix Table A4). The presence of protruding rocks and the old growth forest buffer emerged as the most important predictors and were included in the 95% confidence sets of all species. Furthermore, the young secondary forest and open land buffer variables were included in these model sets for all but one species. The presence of overhanging vegetation, the grain size of the stream bed sediment and the settlement buffer were the least important predictor variables, present in less than half of the eleven 95% confidence sets.

Abundance–suitability relationship

Spearman's rank correlations between log-transformed relative mean abundances observed at the 37 sampling sites and their respective suitability values as predicted by means of logistic regression were significantly positive for all eleven species. Correlation coefficients were generally high (ρ mean = 0.74), ranging from 0.60 to 0.89 (Table 3).

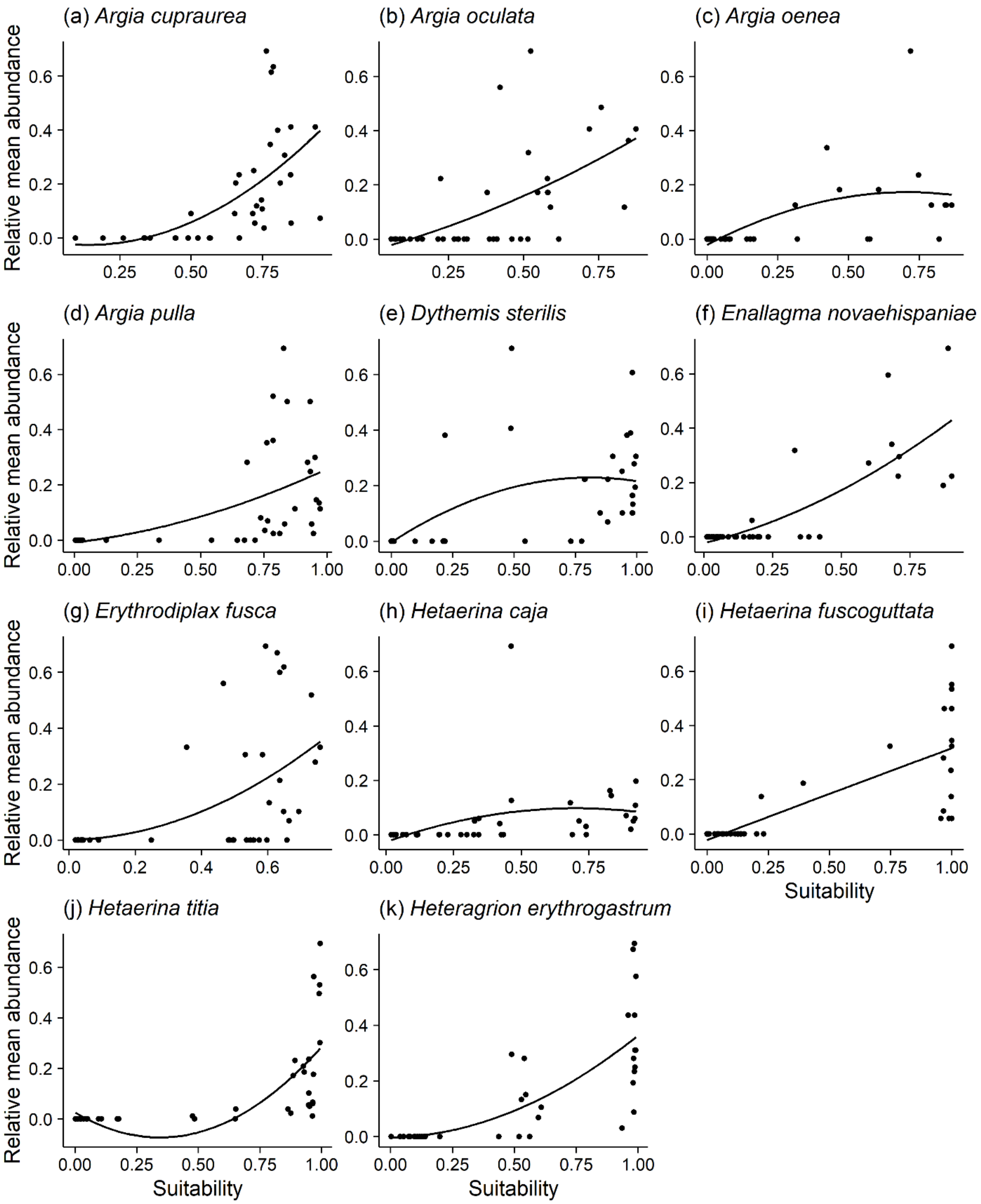

Figure 2. Relationships between log (x + 1)-transformed relative mean abundance and suitability derived from averaged logistic regression models. Black lines represent regression lines of an OLS regressions.

OLS regressions further investigating these AS relationships (Figure 2) were significant for all but one (*Hetaerina caja*; Figure 2h) of the model species. The explanatory power of the significant models was moderate to high (R^2 mean = 0.41, range = 0.25 – 0.64), while it was low ($R^2 = 0.12$) in the non-significant model (Table 3). After examination of the plots, the non-significance of the regression for *Hetaerina caja* appeared to be caused by a single outlier.

Removal of this one outlier resulted in a highly significant regression model ($R^2 = 0.44$, $p < 0.001$); however, further analyses were based on the original model for this species.

Table 3. Relationships between log-transformed relative mean abundances and suitability values derived from averaged logistic regressions models. These relationships are expressed as Spearman's rank correlation coefficient (*ρ*) and the R^2 of an OLS regression. P-values reported for OLS regressions represent the respective global p-values.

Species	Spearman correlation		OLS regression		
	ρ	**p**	**R²**	**F**	**p**
Argia cupraurea	0.77	< 0.001	0.37	9.86	< 0.001
Argia oculata	0.66	< 0.001	0.35	9.12	< 0.001
Argia oenea	0.67	< 0.001	0.34	8.94	< 0.001
Argia pulla	0.74	< 0.001	0.26	5.93	< 0.01
Dythemis sterilis	0.64	< 0.001	0.25	5.78	< 0.01
Enallagma novaehispaniae	0.71	< 0.001	0.64	30.29	< 0.001
Erythrodiplax fusca	0.60	< 0.001	0.25	5.56	< 0.01
Hetaerina caja	0.73	< 0.001	0.12	2.34	0.112
Hetaerina fuscoguttata	0.85	< 0.001	0.57	22.26	< 0.001
Hetaerina titia	0.89	< 0.001	0.46	14.68	< 0.001
Heteragrion erythrogastrum	0.85	< 0.001	0.59	24.26	< 0.001

When considering only abundances-when-present, log-transformed relative mean abundances and suitability values were negatively and positively correlated for five and six species, respectively (Table 4). These correlations were not significant, except for *Hetaerina titia* ($\rho = 0.66$, $p < 0.01$).

The corresponding OLS regressions revealed similar results (Table 4). The AS relationship was significant only for *Hetaerina titia* with moderate explanatory power ($R^2 = 0.34$, $p = 0.023$). For the remaining ten species, the amount of variance explained by these models was substantially reduced when compared to the models including absences (R^2 mean = 0.13, range = 0.01 – 0.31).

Table 4. Relationships between log-transformed relative mean abundances-when-present and suitability. These relationships are expressed as Spearman's rank correlation coefficient (*ρ*) and the R^2 of an OLS regression. P-values reported for OLS regressions represent the respective global p-values.

Species	Spearman correlation		OLS regression		
	ρ	**p**	**R²**	**F**	**p**
Argia cupraurea	0.29	0.172	0.10	1.06	0.364
Argia oculata	−0.02	0.949	0.01	0.04	0.956
Argia oenea	−0.47	0.173	0.24	1.12	0.378
Argia pulla	−0.02	0.920	0.04	0.42	0.662
Dythemis sterilis	−0.26	0.251	0.20	2.34	0.124
Enallagma novaehispaniae	0.09	0.802	0.20	0.89	0.451
Erythrodiplax fusca	−0.25	0.352	0.03	0.20	0.825
Hetaerina caja	0.12	0.655	0.07	0.52	0.607
Hetaerina fuscoguttata	0.38	0.136	0.07	0.50	0.614
Hetaerina titia	0.66	< 0.01	0.34	4.68	< 0.05
Heteragrion erythrogastrum	0.49	0.033	0.31	3.55	0.053

Effects of habitat specialisation

The strength of the AS relationships (considering all abundance, i.e. including abundances = 0) was significantly related to the degree of habitat specialisation across the eleven model species (OLS regression: $F_{(1, 9)} = 8.03$, $p = 0.019$, $R^2 = 0.47$; Figure 3).

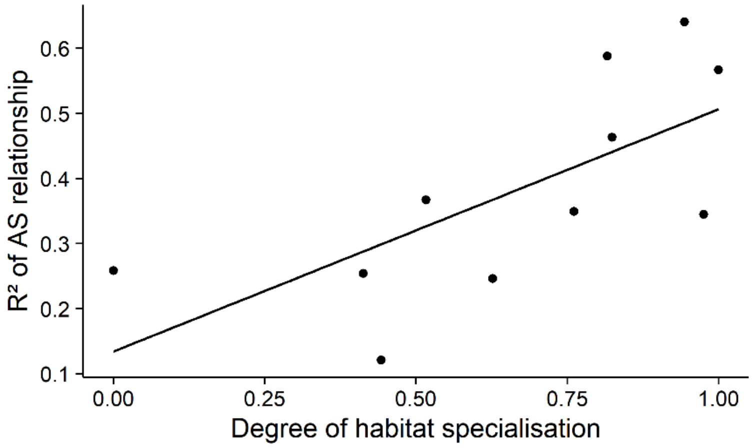

Figure 3. Relationships between the strength of the species' AS relationships (R^2 of models relating abundance to suitability, considering all abundances) and their degree of habitat specialisation. The black line represents the regression line of the OLS regressions.

Discussion

Abundance–suitability relationships

The tropical Odonata species considered for this study exhibit strong abundance–suitability relationships. The degree of correlation found between abundance and suitability was on par with (Gutiérrez et al., 2013) or even exceeding (Filz et al., 2013; Jiménez-Valverde et al., 2009) the correlations previously reported from the few studies exploring these relationships in insects. In addition, regression models relating abundances to suitability were significant for all but one species. In the case of this one species (*Hetaerina caja*), a single outlier was responsible for the non-significant result of the regression. This outlier represented a site at which this species exhibited its maximum abundance, but the model predicted only intermediate suitability. Recalculating the regression without this outlier resulted in a highly significant relationship. Hence, it is plausible that a strong AS relationship exists for this species as well.

Although most relationships were significant, the explanatory power of these relationships was only moderate for most species, with the regression models on average accounting for roughly 38% of the variation in observed abundances. Yet, while some studies report larger R^2 values (de la Fuente et al., 2021; Weber & Grelle, 2012), they still compare favourably to many other studies (Weber et al., 2017). However, most studies assumed linear relationships between abundance and suitability, whereas we considered these relationships to be quadratic. Since neither significance nor explanatory power of AS relationships changed to any meaningful extent when only including a linear term (results not shown), these values should still be comparable.

When excluding unoccupied sites, thus only relating abundances-when-present to suitability, the AS relationships break down for all but one species (*Hetaerina titia*), both in terms of correlation coefficients and regression models. This approach of only considering abundance-when-present was used by some authors (e.g., Pearce & Ferrier, 2001) as they argued that strong correlations when including unoccupied sites indicate good discrimination between presences and absences, rather than the capacity to explain abundance variation (Jiménez-Valverde et al., 2009). Guarino et al. (2012) on the other hand suggested that the non-significance in these cases may instead be caused by the significant reduction in sample size and a concomitant loss of analytical power. There are however cases, in which AS relationships remain strong even when exclusively considering abundances > 0, which suggests that strong AS relationships are not necessarily a consequence of the high discrimination capacity of suitability models (Gutiérrez et al., 2013; Muñoz et al., 2015). Still, further reducing the sample size by omitting unoccupied sites could be the reason for the observed loss of predictive power in this study. Further, this truncation of the data may be counterproductive if the goal is to predict abundances across the whole range of unsuitable to highly suitable habitats. When disregarding unoccupied, i.e., largely unsuitable sites, one cannot expect the resulting relationship to accurately predict abundances across the whole suitability gradient.

Nevertheless, this pattern, as well as the visual examination of abundance–suitability plots, highlight that suitability is only able to explain abundance variation to some extent. This observation has led VanDerWal et al. (2009) to suggest a ‘wedge-shaped’, rather than a linear relationship between abundance and suitability. That is, suitability is only able to predict the upper limit of abundances, while realised abundances can deviate substantially from this upper limit at the most suitable sites but show little variation at less suitable sites. These wedge-shaped relationships have since been reported by multiple studies (Acevedo et al., 2017; Carrascal et al., 2015; Gutiérrez et al., 2013) and although limited sample size may obscure these patterns for the species analysed in this study, some of the abundance–suitability plots (Figure 2) could be interpreted in a way to suggest that tropical odonates may also follow this pattern. Since carrying capacity seems to be mostly positively related to suitability (Thuiller et al., 2014), it has been suggested, that the upper limit predicted by wedge-shaped AS relationships could be related to carrying capacity (Muñoz et al., 2015). A variety of different factors may then be expected to be responsible for the deviations of observed abundances from this upper limit, thus reducing the ability to accurately predict abundance from suitability.

Species interactions may weaken AS relationships, as strong competitors could prevent species from occupying the most suitable habitats, forcing them to migrate into less suitable habitats (McGill et al., 2006). Source-sink dynamics could further obscure AS relationships, with high abundances in sink habitats caused by immigration from source habitats where reproduction is high (Van Horne, 1983). Both processes could lead to unexpectedly high and low abundances in unsuitable and highly suitable habitats, respectively but exploring species interactions and potential metapopulation dynamics lies beyond the scope of this study. This pattern could further be caused by dispersal limitation, when species are unable to colonise suitable habitats and are therefore restricted to less suitable habitats (Pulliam, 2000; VanDerWal et al., 2009). Indeed, Jiménez-Valverde et al. (2009) noticed that more vagile arthropods tend to exhibit stronger AS relationships. Similarly, de la Fuente et al. (2021) reported that dispersal capacity was significantly and positively related to the predictive power of AS relationships in tropical vertebrates. Although little is known about the dispersal capacity of the Odonata species treated in this study, it has been shown that dispersal limitation can affect an odonate's ability to colonise newly formed habitats (McCauley, 2006). In general, Odonata are still highly proficient fliers (Corbet, 2004), hence, when considering the spatial scale of this study, an effect of dispersal limitation on the observed AS relationships appears to be highly unlikely.

Spatial scale itself could influence the strength of AS relationships by not investigating this relationship across a wide enough range of different habitats (He & Gaston, 2007; Nielsen et al., 2005). At small spatial scales, environmental variables used for modelling suitability may only vary within a small range of values, consequently reducing the predictive power of suitability models (Van Couwenberghe et al., 2013; Weber et al., 2017). Yet, when comparing reported correlations between abundance and suitability, Weber et al. (2017) did not find significant differences between studies conducted over either small or large proportions of a species' range. While the spatial extent of this study is considerably smaller than that of the studies included in this meta-analysis, we expect a lack of variation in predictor variables to not be an issue. This problem should rather affect climatic variables, which are available at much coarser spatial resolutions compared to the fine-scale environmental variables utilised in this study. As the study area comprises a variety of different waterbodies and surrounding habitats, these fine-scale environmental variables do vary substantially even within this relatively small study area.

The choice of variables for modelling suitability can also sway observed AS relationships, as some variables may not be directly or only weakly related to species occurrence and abundance (Weber et al., 2017). While a variety of different fine-scale environmental variables that could be assumed to be relevant for Odonata occurrences were considered in this study, it predominantly focused on variables more likely to affect adults rather than larvae. However, a habitat must meet the requirements of all stages in the life cycle of an odonate (Corbet, 2004). Therefore, including additional variables concerning the properties of the waterbodies themselves, e.g., temperature, salinity, pH, oxygen content and the concentrations of pollutants and pesticides, are likely to strengthen observed AS relationships.

Abundance fluctuations and detectability of a species have also been suggested to affect whether observed abundances are a reasonable measure for real abundances (Jiménez-Valverde et al., 2009; Pearce & Ferrier, 2001; Van Horne, 1983). For this study, sampling sites were visited multiple times to collect data on Odonata abundances and these abundances were then averaged for each site. Therefore, we expect that a species' detectability and the temporal variability of abundances contribute only marginally to the deviations between predicted and observed abundances.

While the aforementioned exclusion of variables indicative of larval habitat quality potentially reduced the quality of suitability models, thus likely weakening the resulting AS relationships, we suspect sample size, i.e., the number of sampled sites, to be the biggest limitation of this study. Even though it has been demonstrated that sample size does not significantly affect AS relationships (Dallas & Hastings, 2017), de la Fuente et al. (2021) found that sample size and the strength of AS relationships were negatively, although not significantly, related. Still, even with our limited sample size, we could demonstrate that tropical odonates show strong correlations between observed abundance and model-derived suitability and that AS relationships explain at least moderate amounts of abundance variation. The inclusion of fine-scale environmental variables has likely contributed to finding stronger AS relationships than previously reported for arthropods (Filz et al., 2013; Jiménez-Valverde et al., 2009). Only Gutiérrez et al. (2013), who also utilised fine-scale environmental variables, reported even stronger AS relationships, which could potentially be ascribed to the larger sample size in their study.

While a substantial amount of variance is left unexplained, the fact remains that occurrence data is much more readily available than abundance data. Abundance models are plagued by many of the same problems discussed above (e.g., species interactions, metapopulation dynamics, temporal variability) and can be outperformed by occurrence models in terms of their ability to accurately predict abundances (Guarino et al., 2012; Gutiérrez et al., 2013; Pearce & Ferrier, 2001). Additionally, both species occurrences and abundances appear to be controlled by similar environmental variables (Carrascal et al., 2015; Gutiérrez et al., 2013). Hence, until abundance models can significantly outperform occurrence models, strong AS relationships suggest, that occurrence can be a reasonable, efficient proxy to predict abundance.

Effect of habitat specialisation on the strength of AS relationships

It has previously been suggested that the species' degree of specialisation may also influence whether species exhibit either weak or strong AS relationships (Jiménez-Valverde et al., 2009; Nielsen et al., 2005). Stronger AS relationships in specialist compared to generalist species were assumed, as specialist species have narrower ecological niches, which restrict them to occur in a limited number of habitats (Brown, 1984). Accordingly, habitat generalists have been shown to be more widespread than habitat specialists. Verberk et al. (2010) further demonstrated that specialists can occur in higher abundances compared to generalists. Indeed, studies investigating AS relationships in single, specialist species found strong relationships between abundance and suitability (Muñoz et al., 2015; Weber & Grelle, 2012).

To our knowledge, only one study has yet directly explored the effect of habitat specialisation on AS relationships. Carrascal et al. (2015) related a measure of habitat niche breadth to AS model residuals and found that AS relationships generally overestimated abundances for generalist species, which exhibited a larger mismatch between predicted and observed abundances than in specialist species. Factors other than the environmental variables included in the models may be responsible for shaping realised abundances of generalists, therefore AS relationships appeared to be stronger for specialist rather than generalist species (Carrascal et al., 2015). These findings are corroborated by the results of this study, as we found the species' degree of habitat specialisation to be a significant predictor for the strength of AS relationships. This relationship explains 47% of the variation in the strength of AS relationships. While a large amount of variation is still left unaccounted for, the explanatory power of habitat specialisation is substantial, highlighting the important role habitat specialisation may play in determining the strength of AS relationships.

Conclusion

Overall, this study demonstrates that most of the analysed tropical Odonata species exhibit strong correlations between their abundances and model-derived suitability values. Yet, the explanatory power of abundance–suitability relationships is only moderate for most species. Sample size limitations, as well as the non-consideration of potentially important indicators of larval habitat quality are presumed reasons for the observed deviations between observed and predicted abundances. Further, this study provides evidence, that a species' degree of habitat specialisation affects the strength of its abundance–suitability relationship, with abundances of specialists being more tightly linked to suitability than those of generalist species.

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Appendix A

Table A1. Species recorded across the three surveys, including suborder and family association, as well as the total number of recorded individuals and the number of occupied sites (excluding singletons).

Species	Number of recorded indivduals	Number of occupied sites
Anisoptera		
Gomphidae		
Agriogomphus tumens	1	–
Perigomphus pallidistylus	1	–
Progomphus pygmaeus	1	–
Libellulidae		
Anatya guttata	1	–
Brechmorhoga nubecula	3	–
Dythemis nigra	25	6
Dythemis sterilis *	173	22
Elasmothemis cannacrioides	9	2
Erythemis peruviana	2	–
Erythemis plebeja	3	1
Erythrodiplax fervida	9	1
Erythrodiplax fusca *	191	16
Erythrodiplax umbrata	2	1
Macrothemis imitans	1	–
Macrothemis inequiunguis	2	–
Miathyria simplex	1	–
Micrathyria aequalis	3	–
Nephepeltia phryne	8	1
Oligoclada heliophila	5	2
Orthemis biolleyi	1	–
Orthemis discolor	28	9
Orthemis ferruginea	8	2
Orthemis levis	1	–
Perithemis domitia	2	1
Perithemis electra	13	4
Perithemis tenera	5	1
Rhodopygia hinei	4	–
Uracis imbuta	15	4
Erythrodiplax kimminsi	3	1
Zygoptera		
Calopterygidae		
Hetaerina caja *	163	16
Hetaerina capitalis	1	–
Hetaerina fuscoguttata *	214	17
Hetaerina occisa	965	32
Hetaerina sempronia	2	–
Hetaerina titia *	549	21
Coenagrionidae		
Acanthagrion trilobatum	14	4
Argia adamsi	44	6
Argia carolus	35	8
Argia cupraurea *	377	23

Table A1. Continued.

Species	Number of recorded indivduals	Number of occupied sites
Coenagrionidae (continued)		
Argia frequentula	8	2
Argia indicatrix	5	1
Argia oculata *	97	15
Argia oenea *	43	10
Argia pocomana	1	–
Argia pulla *	447	22
Argia translata	65	6
Argia underwoodi	1	–
Enallagma novaehispaniae *	127	10
Ischnura capreolus	55	6
Ischnura ramburii	4	–
Leptobasis vacillans	7	1
Mecistogaster modesta	1	–
Mecistogaster ornata	1	–
Psaironeura angeloi	9	2
Megapodagrionidae		
Heteragrion erythrogastrum *	686	19
Perilestidae		
Perissolestes remotus	1	–
Philogenidae		
Philogenia championi	3	1
Platystictidae		
Palaemnema reventazoni	2	1
Polythoridae		
Miocora semiopaca	1	–
Protoneuridae		
Neoneura esthera	28	4
Protoneura amatoria	47	7
Protoneura sulfurata	8	2

* Species for which suitability models were calculated

Table A2. Correlations among environmental variables. Values represent Spearman's rank correlation coefficient (*ρ*) for correlations including the ordinal variables (i.e., PWD, PR, OV, RB, GSS), and Pearson's correlation coefficient (*r*) otherwise. Correlation coefficients ≥ 0.7 or ≤ −0.7 are highlighted in bold.

Variable	PWD	PR	OV	RB	GSS	RW	FV	VH	CC	OGF	YSF	OPP	OL	SET
PR	−0.04													
OV	0.07	0.33												
RB	0.09	0.32	0.03											
GSS	−0.15	0.29	0.17	−0.04										
RW	0.40	−0.08	−0.18	0.30	−0.11									
FV	−0.16	0.02	0.26	−0.04	0.37	0.26								
VH	0.18	0.36	0.44	0.22	0.43	−0.06	0.01							
CC	−0.20	0.43	0.49	0.06	0.29	−0.43	−0.04	**0.73**						
OGF	0.15	0.66	0.26	0.25	0.31	−0.33	−0.34	0.57	0.64					
YSF	−0.07	−0.23	−0.09	0.24	0.03	0.45	0.27	0.10	−0.13	−0.42				
OPP	−0.05	−0.47	0.18	−0.30	−0.17	−0.01	0.15	−0.37	−0.31	−0.48	−0.31			
OL	−0.07	−0.37	−0.09	−0.24	−0.23	0.16	0.12	−0.38	−0.47	−0.62	0.13	0.24		
SET	−0.06	0.04	−0.05	−0.06	−0.03	−0.13	−0.12	0.02	0.05	−0.03	−0.04	−0.26	−0.09	
LIN	0.07	−0.25	−0.04	−0.54	0.03	0.23	0.18	−0.15	0.07	−0.15	−0.03	0.09	−0.01	0.15

Variable abbreviations:

PWD … Protruding woody debris
PR … Protruding rocks
OV … Overhanging vegetation
RB … Riverbank
GSS … Grain size of stream bed sediment
RW … River width
FV … Flow velocity
VH … Height of surrounding vegetation
CC … Canopy cover
OGF … Old growth forest in buffer
YSF … Young secondary forest in buffer
OPP … Oil palm plantation in buffer
OL … Open land in buffer
SET … Settlements in buffer
LIN … Linearity of river section

Table A3. Principal component analysis (PCA) based on the 14 environmental variables. Values represent the loadings of the first five principal components used for calculating the species' habitat specialisation, as well as the eigenvalues of and the variance explained by the individual principal components.

Variable	**Principal components**				
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
PWD	0.26	0.12	−0.21	0.03	0.80
PR	0.83	−0.15	0.36	−0.06	−0.26
OV	0.58	0.15	−0.14	0.24	0.26
RB	0.06	0.71	0.09	−0.27	0.03
GSS	0.32	0.34	0.75	0.14	0.00
RW	−0.31	0.77	−0.03	−0.02	0.14
FV	−0.05	0.62	0.54	0.14	0.08
VH	0.67	0.27	−0.43	0.13	0.10
OGF	0.89	−0.08	−0.04	−0.16	−0.06
YSF	−0.24	0.64	−0.26	0.12	−0.29
OPP	−0.53	−0.37	0.36	−0.23	0.45
OL	−0.64	0.07	−0.16	0.26	−0.10
SET	0.07	−0.04	−0.25	0.63	−0.02
LIN	−0.07	−0.26	0.42	0.66	0.09
Eigenvalue	3.30	2.35	1.71	1.17	1.12
Variance explained	0.24	0.17	0.12	0.08	0.08
Cumulative variance explained	0.24	0.40	0.53	0.61	0.69

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Table A4. The number of models comprising the 95% confidence set of each species, as well as the predictors included (+) in these model sets.

Species	Number of models	PWD	PR	OV	RB	GSS	RW	FV	VH	OGF	YSF	OPP	OL	SET	LIN
Argia cupraurea	39	+	+		+	+	+	+	+	+	+	+	+	+	+
Argia oculata	38	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Argia oenea	11		+		+		+	+	+	+	+	+	+	+	+
Argia pulla	14	+	+	+			+		+	+	+	+	+		+
Dythemis sterilis	3	+	+							+	+		+		
Enallagma novaehispaniae	29	+	+	+	+	+		+	+	+	+	+	+		+
Erythrodiplax fusca	27	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Hetaerina caja	14	+	+		+		+		+	+	+	+	+		
Hetaerina fuscoguttata	8	+	+		+		+		+	+	+	+			
Hetaerina titia	5	+	+		+		+			+			+		
Heteragrion erythrogastrum	15		+	+		+	+		+	+	+	+	+		+

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Appendix B

Zusammenfassung

Nischenmodelle werden in Zeiten des globalen Wandels immer wichtiger, um die Verbreitung von Arten zu untersuchen. Diese Modelle basieren meist auf Inzidenz- und nicht auf Abundanzdaten. Für viele Anwendungen ist die Abundanz jedoch der relevantere Parameter. Da solche Daten aber nur selten verfügbar sind, könnte die Vorhersage von Abundanzen durch die Habitateignung, die aus entsprechenden Inzidenz-basierten Modellen abgeleitet werden kann, zur Lösung dieses Problems beitragen. Im Allgemeinen scheint eine Beziehung zwischen Abundanz und Habitateignung zu existieren, ihre Vorhersagekraft variiert jedoch stark. In dieser Studie wird die Beziehung zwischen Abundanz und Habitateignung in tropischen Libellen untersucht. Die Habitateignung wurde mit Hilfe feinskaliger Umweltvariablen modelliert und dann mit den beobachteten Abundanzen in Beziehung gesetzt. Zusätzlich wurde untersucht, ob der Grad der Habitatspezialisierung der einzelnen Arten die Stärke dieser Beziehungen bestimmt. In zehn der elf untersuchten Libellenarten standen Abundanz und Habitateignung in einem signifikantem Zusammenhang, die Erklärungskraft dieser Beziehungen war jedoch für die meisten Arten nur mäßig. Die Stärke dieser Beziehungen stand außerdem in einem signifikantem Zusammenhang mit dem Grad der Habitatspezialisierung. Dies deutet darauf hin, dass Inzidenz-basierten Modelle verwendet werden können, um Abundanzen abzuleiten. Es ist jedoch Vorsicht geboten, da ihre Vorhersagekraft sehr variabel ist und von zahlreichen Faktoren beeinflusst werden kann. Wie für den Effekt der Habitatspezialiserung gezeigt.

Schlagwörter: Abundanz, Costa Rica, Habitateignung, Habitatspezialisierung, Libellen, Nischenmodelle, Odonata, Tropen