

Research



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Why do bugs perish? Range size and local vulnerability traits as surrogates of Odonata extinction risk

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Despite claims of an insect decline worldwide, our understanding of extinction risk in insects is incomplete. Using bionomic data of all odonate (603 dragonflies and damselflies) North American species, we assessed (i) regional extinction risk and whether this is related to local extirpation; (ii) whether these two patterns are similar altitudinally and latitudinally; and (iii) the areas of conservation concern. We used geographic range size as a predictor of regional extinction risk and body size, thermal limits and habitat association as predictors of local extirpation. We found that (i) greater regional extinction risk is related to narrow thermal limits, lotic habitat use and large body size (this in damselflies but not dragonflies); (ii) southern species are more climate tolerant but with more limited geographic range size than northern species; and (iii) two priority areas for odonate conservation are the cold temperate to sub-boreal northeastern USA and the transversal neo-volcanic system. Our approach can be used to estimate insect extinction risk as it compensates for the lack of abundance data.

1. Introduction

Contemporary species extinction rates are rising abruptly as they are driven mostly by direct anthropogenic pressures [1]. Although these extinctions are typically non-random [2], our capacity to predict which organisms are more vulnerable to extinction is still weak, particularly in poorly known taxa [3,4]. Nonetheless, it is well known that two processes that operate at different spatial scales render species to extinction: a decline in both geographic distribution (large scale) and population abundance (local scale) [5–7]. Given the current extinction crisis, we need to identify intrinsic ecological traits that predict species' susceptibility to disappear [8–10]. This identification should be accompanied by the recognition of areas where conservation action should take place [11].

Insects are one of the most diverse biological groups, and the projections of species extinction rates are dramatically underestimated [3,4]. This is largely due to the paucity of information in regards to drivers and historical patterns of extinction, and even data on basic biology [4]. Consequently, extremely few (less than 2%) insect species have been classified into any extinction risk categories, although approximately 40% of those assessed by the International Union for Conservation of Nature (IUCN) are considered least threatened [12]. This implies an urgent need for setting risk criteria to allow protection of these animals [13,14] based on the predictors of extinction risk. In this paper, we have aimed to predict such risk for a model freshwater insect group in conservation [15] based on geographic range size (GRS) and key traits of local vulnerability (body size, climatic tolerances and breeding habitat).

GRS—the geographic boundary where a particular species occurs [16]—varies considerably among species. Note that GRS is the most common and straightforward metric to evaluate regional extinction risk: the smaller the GRS, the greater the susceptibility to ecological disturbance and environmental change and thus higher the risk of extinction [17]. Regional endemic species, for example, would be more vulnerable than wide-ranging species to regional environmental change. The relationship between GRS and extinction risk is particularly important for insects which are habitat or feeding specialists [18,19]. In fact, GRS may be linked to traits that can inform on vulnerability of species to local extirpation. Indeed, trait-based approaches can be a powerful tool for inferring vulnerability [10], especially for insects given the difficulties of sampling and shortage of abundance data [13]. In this regard, trait-based models have attributed local population declines of insects to body size [20], thermal limits [21] and breeding habitat [22].

The relationship between GRS and local vulnerability traits of species is not simple as neither is the relationship among those traits. Body size is related to dispersal ability and is involved in the regulation of body temperature [23]. According to this, large-bodied aquatic arthropod species tend to occur at higher latitudes, whereas terrestrial species mainly show the opposite pattern [21,24]. According to this, greater dispersal ability allows organisms to ‘escape’ unfavourable conditions, thereby lowering their regional extinction risk and their vulnerability to extirpation. However, large-bodied species tend to have low average population densities locally, which render these species more vulnerable to local extinctions [25]. Thermal limits are important for post-dispersal establishment, and species that evolved under broad climatic ranges have larger thermal limits and tend to concentrate at northern latitudes [21,24] and higher elevation [26]. Locally, these species may tolerate disturbance better than species with narrow thermal limits adapted to more stable climatic conditions [24,26]. Following local ecological disturbance, habitat generalists are more likely to persist than specialist species [27]. In other words, the population of a habitat specialist species tends to decline, and eventually this will be mirrored in the reduction of the GRS [28]. Although complicated, the connections of body size, thermal limits and breeding habitat with population abundance makes these traits good proxies of how likely a species will disappear locally and, with enough local predictions, regionally or range wide.

Insects comprise about 60% of known animal diversity in the freshwater realm [29]. Odonata—dragonflies (suborder Anisoptera) and damselflies (suborder Zygoptera)—are model freshwater taxa for conservation [15] with a limited deficit of taxonomic knowledge [30] and relatively high global species richness [31]. The two suborders are distinct in their morphology, behaviour and ecophysiology [32], such that the dragonflies are generally larger with greater dispersal ability and heliothermic tendency compared with damselflies [33]. Although 56% of odonate species are listed by the IUCN around the world [17,34], 25% of these species have been categorized as data deficient. Yet information on GRS, body size, climatic tolerances and breeding habitat are available for most of the species [35–37] thus enabling trait-based assessment of extinction risk.

Our general aim was to evaluate regional extinction risk and local vulnerability of insects from North America, and the relationship between the two. More specifically, we were

interested in the following questions. Are Odonata species at high risk of regional extinction also at high risk locally? Are the results similar for the suborders (Anisoptera and Zygoptera)? Are the latitudinal and altitudinal patterns in regional extinction risk and local vulnerability similar? How can this information help for Odonata conservation? We predicted a negative relationship between regional extinction risk and each local vulnerability trait (body size, thermal limits, habitat association). Additionally, we expected northern species to collectively show larger body size and southern species and high-altitude species to collectively exhibit narrower climatic tolerance. We used the results to discuss conservation priority areas [11] for Odonata in North America.

2. Material and methods

(a) Regional extinction risk index

To quantify the GRS as a surrogate of regional extinction risk, we used two measures, the extent of occurrence (EOO) and the area of occupancy (AOO). The former is a measure of the species’ range limits and hence of their vulnerability to threats across geographic space [38]. The latter measures the area actually occupied by the species as a function of the scale (e.g. spatial resolution). Both EOO and AOO were calculated based on occurrence data (records) for each species. The records were obtained from OdonataCentral, a storage and distribution hub for adult odonate records throughout North America [30], and from CONABIO [39], a storage site for, mainly, Mexican diversity. We removed duplicated and incorrectly georeferenced records, rendering a total of 300 896 records (97 398 Canada; 65 647 Mexico; 137 851 United States) for 603 species (400 Anisoptera and 203 Zygoptera; listed in electronic supplementary material, table S1). Synonyms were checked using the Integrated Taxonomic Information System (<http://www.itis.gov>, retrieved 15 March 2017).

We overlaid odonate records on Level II terrestrial ecoregions of North America (www.cec.org) and selected for analysis those regions with a completeness higher than 50%. Completeness was calculated using the ICE and Chao2 nonparametric estimators as implemented in EstimateS v. 8.2 [40]; these estimators are recommended for incidence data [41]. We calculated EOO as the area (km²) of a minimum convex polygon surrounding all occupied territory of North America, using the *gConvexHull* command in the *rgeos* package in the R statistics software [42]. We used AOO to distinguish between species that are widely distributed throughout their EOO and those with disjunct distributions [18]. For this, we first associated the species’ records to ecoregions of North America then we used the number of occupied ecoregions across each species’ distribution to represent AOO [18]. We used this measurement to help distinguish between species that are widely distributed throughout their range and those with disjunct or highly fragmented distributions [17]. Second, we constructed an extinction risk index based on the average of EOO and AOO and scaled from 0 to 1 [5], where values closer to 0 means that species has the greatest GRS and lowest regional extinction risk, while values closer to 1 means that the species has the smallest GRS and highest regional extinction risk. In this way, we used GRS as the values of proportions between studied species more than raw measures to avoid bias from incomplete and uneven sampling [13].

(b) Vulnerability to local extirpation

Considering odonate physiology, we defined the thorax length (mm) as the appropriate proxy of adult body size. Because thoracic musculature is a key trait for both weight acquisition and energy assimilation [43], the thorax serves as the functional basis for

thermoregulation [23] and dispersal [43]. Furthermore, thorax length is correlated with weight at emergence in odonates [44,45]. Data on adult thorax size were mainly extracted for each species from the Encyclopedia of Life [46]. These were complemented with other sources such as <http://natuurtijdschriften.nl/natuur> and www.odonatephenotypicdatabase.org. Climatic tolerance was evaluated using a proxy of thermal tolerance, the average isothermality values (BIO3) across each species' EOO [47]. The values of isothermality (BIO3) were taken from bioclimatic variables [48]. Habitat specialization was categorized by breeding habitat: lentic, lotic or no preference [46]. Subsequently, local vulnerability of species was evaluated scaling the values of thorax size, thermal tolerance and breeding habitat (no preference = 0.33, lentic = 0.66, lotic = 1) from 0 to 1. Species with a small thorax, wider climatic tolerance or no habitat preference would be the least vulnerable (value = 0), whereas the most vulnerable species (value = 1) would have a large thorax, narrower climatic tolerance or preference for lotic habitat. We assume that lotic species are more vulnerable to extirpation because they generally have smaller range sizes and poorer dispersal ability compared to lentic species [28,49].

(c) Statistical analysis

A super-tree was generated from Odonata mega-tree [50] using the software Phylomatic version 3 [51]. Families were dated in Phylocom [52] using the *bladj* algorithm and taking into account the dating dates proposed by Davis *et al.* [53]. For each continuous trait (body size, climatic tolerance), we calculated Pagel's λ to quantify the strength of phylogenetic signal from zero (no signal) to one [54]. We controlled for significant signal in subsequent modelling.

We evaluated the relationship between regional extinction risk (GRS index) and each metric of local vulnerability for all 603 species. As the occurrence records were collected without a specific sampling design, they contain a variety of biases. To account for these biases, we estimated the relationship between local extirpation and regional extinction using an approach based on Bayesian occupancy modelling [55]. A Bayesian approach to generalized linear mixed models (GLMM) inference offers several advantages over frequentist and information-theoretic methods, particularly when datasets are highly informative and scarce a-prior knowledge is assumed (i.e. when the priors are weak). The Bayesian approach draws conclusions based on a set of weighted models, rather than a single best model. Also, it provides confidence intervals on GLMM parameters (and hence tests of whether those parameters could plausibly equal to zero) in a way that naturally averages the uncertainty of both the fixed and random effect parameters [56]. Finally, due to the non-independence of species as a consequence of their shared evolutionary history, we used statistical analyses based on phylogenetic relationship data to incorporate this dependency in our statistical analyses. Thus, we used phylogenetic Bayesian regression mixed models (PBRMM) [56] of the GRS index in response to each local vulnerability metric, with a lognormal error distribution and species as random factor to account for phylogenetic dependency. We used a matrix covariance structure using our Odonata phylogeny to control for shared evolutionary history. We chose to use the lognormal error distribution as recommended for a linear or exponential regression and with data values between 0 and 1 [57]. All statistical analyses were conducted using R v. 3.5 [42]. Models were implemented using the *brms* package v. 2.4.0 [58], and the *sjstats* package v. 0.17.0 [59] was used for Bayesian inference on the magnitude of a model's parameter value.

We produced $1^\circ \times 1^\circ$ gridded maps representing the regional extinction risk and local vulnerability (thorax size, thermal tolerance, breeding habitat) by suborder [10]. We used GLMM to test the relationship between extinction risk and local vulnerability within 1° bands of latitude (ranging from 14 to 69°N) and 100 m

increments of elevation (ranging from 0 to 3700 m.a.s.l.). This method suffers from the lack of statistical independence, because the average trait values for different latitudinal bands or elevation ranges are influenced by the same species in adjacent bands or ranges; therefore, we used ecoregions of North America as a random factor.

3. Results

Scores for extinction risk and local vulnerability for all 603 species are found in electronic supplementary material, table 1. All but two ecoregions (out of 50 total) resulted in a completeness higher than 50%. Lambda (λ) was significantly different from zero for all traits associated with extinction risk and local vulnerability, indicating a phylogenetic signal. Therefore, shared evolutionary history was controlled in the phylogenetic models.

(a) Extinction risk and vulnerability to local extirpation

Regional extinction risk and thorax size were positively related in Zygoptera but not Anisoptera (figure 1*a,d*; table 1). Although larger zygopterans showed a higher extinction risk than smaller zygopterans, most species were of small size (0.4 or less) with high variation in extinction risk (figure 1*d*). As expected, regional extinction risk and thermal tolerance were negatively related, particularly in the Zygoptera (figure 1*b,e*; table 1). Regional extinction risk was higher for lotic-breeding Zygoptera and Anisoptera than for lentic and generalist species (figure 1*c,f*; table 1). The lentic and generalist groups did not noticeably differ from each other (table 1).

(b) Geographical patterns of regional extinction risk and local vulnerability

Regional extinction risk broadly increased from north to south in both suborders (figure 2*a,b*). Thorax size showed no clear latitudinal pattern in either suborder (figure 3*a,d*) whereas thermal tolerance declined with increasing latitude (figure 3*b,e*). The patterns of regional extinction risk are opposite with the proportionately greater numbers of thermally tolerant species to the south (figures 2 and 3*b,e*). There were few places with relatively low regional extinction risk (less than 0.5 index or cooler map colours) at the southern half of Mexico which supports a proportionately high number of lotic species (figure 3*c,f*), which revealed a markedly high regional extinction risk and local vulnerability.

(c) Relationships to latitude and elevation

Latitude and elevation were significantly related with regional extinction risk in both suborders. Extinction risk increased for both suborders with decreasing latitude and elevation (tables 2 and 3; figure 2). Latitude related positively to thorax size of Anisoptera (table 2) and negatively to Zygoptera (table 3), whereas elevations did not relate with the thorax size of Anisoptera. Conversely, the size of Zygoptera decreased at higher elevations (table 3). Climatic vulnerability increased in both suborders at higher elevations and latitudes (tables 2 and 3). Latitude also significantly influenced species' breeding habitat with greater vulnerability (i.e. lotic tendency) over decreasing latitude and elevation in Anisoptera and Zygoptera (tables 2 and 3).

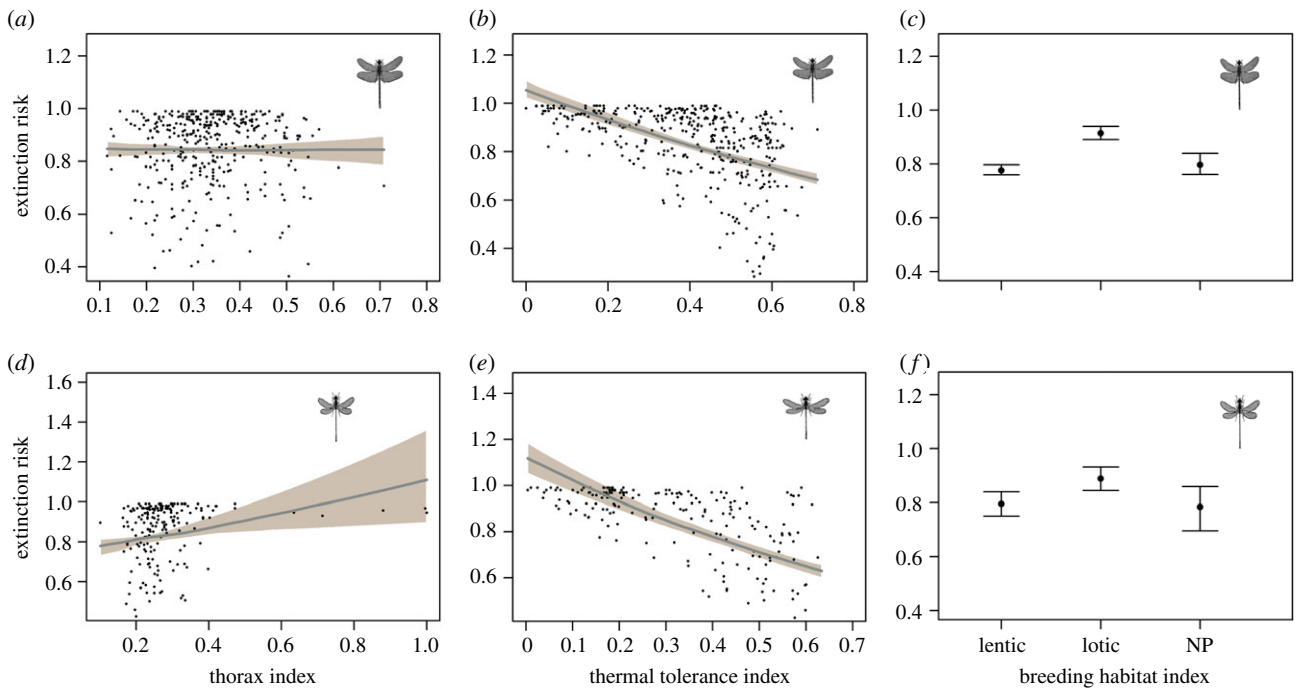


Figure 1. Association between traits linked to local habitat vulnerability change with regional extinction risk for both odonata suborders. Relationship between the regional extinction risk of Anisoptera with (a) thorax size, (b) thermal tolerance and (c) breeding habitat; regional extinction risk of Zygoptera with (d) thorax size, (e) thermal tolerance and (f) breeding habitat. Trend line represents a Bayesian normal linear model fit, with the posterior 95% credible and predictive intervals represented as shading.

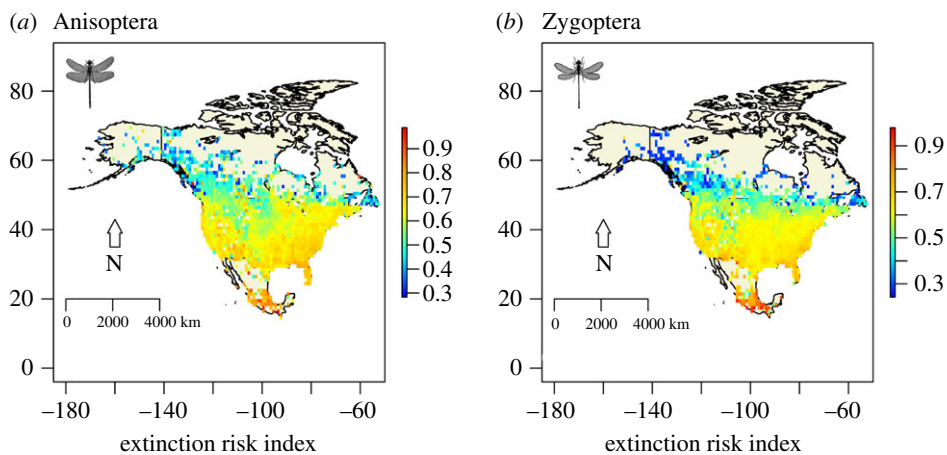


Figure 2. One-degree grid maps showing regional extinction risk distribution in North America for both suborders of Odonata. (Online version in colour.)

Table 1. Phylogenetic Bayesian regression mixed models that examine the relationship of extinction risk with local vulnerability metrics for each odonate suborder (Anisoptera and Zygoptera). Model averaged estimates of parameters (β), standard errors (s.e.) and 95% CI are shown. The parameters for which the 95% credible interval (CI) did not include 0 are considered as the influential parameters and are shown in italic text.

traits associated with habitat change vulnerability	β	s.e.	lower CI	upper CI	pseudo- R^2
Anisoptera					
thorax size	-0.03	0.08	-0.21	0.11	0.3
thermal tolerance	<i>-0.62</i>	<i>0.06</i>	<i>-0.71</i>	<i>-0.48</i>	<i>0.52</i>
breeding habitat (lotic)	<i>0.16</i>	<i>0.02</i>	<i>0.13</i>	<i>0.19</i>	<i>0.42</i>
breeding habitat (no preference)	0.03	0.03	-0.02	0.08	
Zygoptera					
thorax size	<i>0.42</i>	<i>0.15</i>	<i>0.18</i>	<i>0.67</i>	<i>0.48</i>
thermal tolerance	<i>-0.88</i>	<i>0.08</i>	<i>-1.07</i>	<i>-0.72</i>	<i>0.68</i>
breeding habitat (lotic)	<i>0.12</i>	<i>0.05</i>	<i>0.04</i>	<i>0.22</i>	<i>0.45</i>
breeding habitat (no preference)	-0.01	0.04	-0.09	0.04	

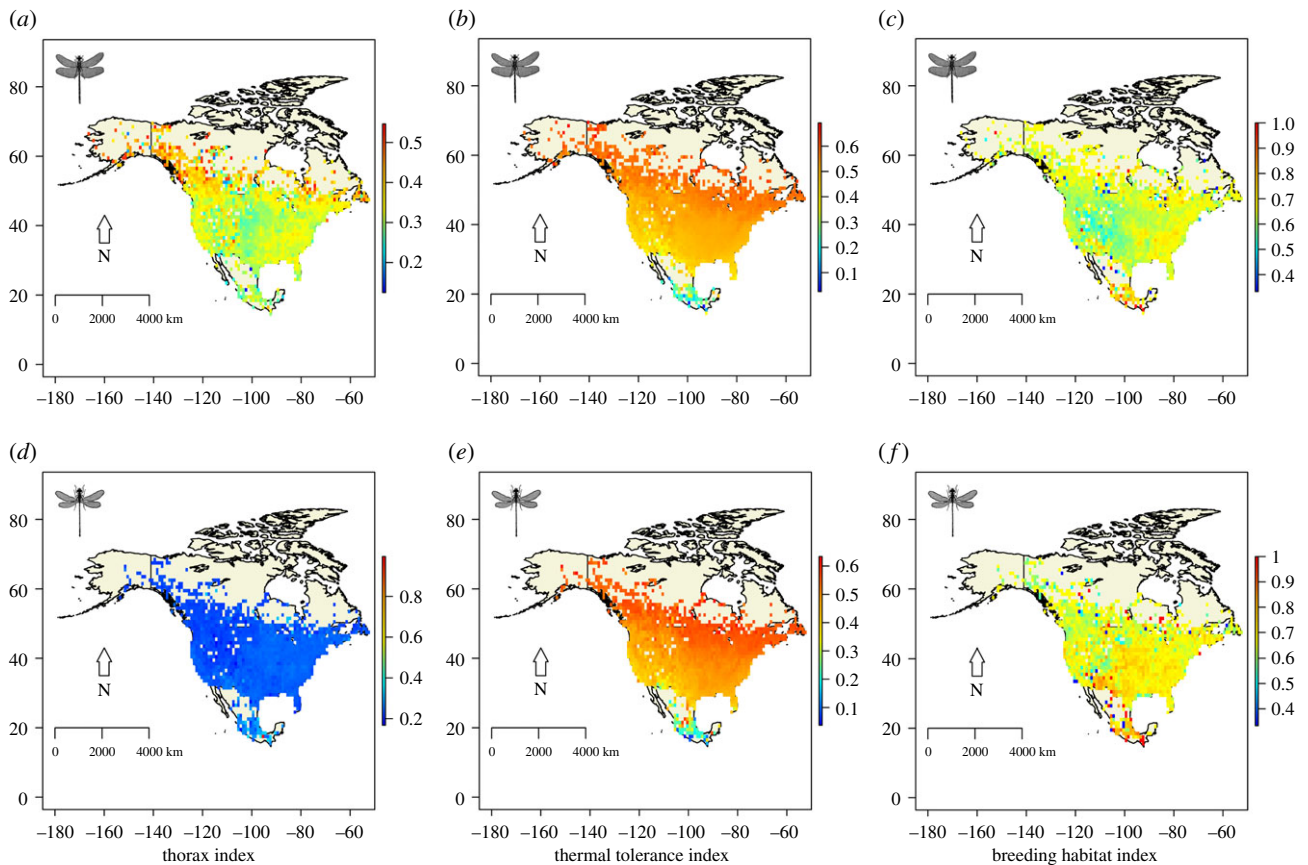


Figure 3. One-degree grid maps showing local vulnerability trait distribution in North America for both suborders of Odonata. For Anisoptera: (a) thorax size, (b) thermal tolerance and (c) breeding habitat. For Zygoptera: (d) thorax size, (e) thermal tolerance and (f) breeding habitat. (Online version in colour.)

Table 2. Generalized linear mixed models of regional extinction risk and local vulnerability traits for 400 Anisoptera species in relation with latitude and elevation gradients throughout North America, accounting for ecoregion (intercept random effect). Significant values appear in *italic*.

local vulnerability traits	covariate	χ^2	slope	s.e.	<i>p</i>
thorax size	latitude	<i>106.95</i>	<i>0.002</i>	<i>0.0002</i>	<i><0.001</i>
	elevation	1.78	3.00×10^{-6}	2.00×10^{-6}	0.18
thermal tolerance	latitude	<i>637.56</i>	<i>0.004</i>	<i>0.0001</i>	<i><0.001</i>
	elevation	29.56	9.00×10^{-6}	1.00×10^{-6}	<i><0.001</i>
breeding habitat	latitude	6.86	<i>-0.0009</i>	<i>0.0003</i>	<i><0.01</i>
	elevation	0.3	-2.00×10^{-6}	4.44×10^{-6}	0.57
extinction risk index	latitude	<i>575.39</i>	<i>-0.007</i>	<i>0.0003</i>	<i><0.001</i>
	elevation	59.95	-3.00×10^{-5}	4.00×10^{-6}	<i><0.001</i>

Table 3. Generalized linear mixed models of regional extinction risk and local vulnerability traits for 203 Zygoptera species in relation with latitude and elevation gradients throughout North America, accounting for ecoregion (intercept random effect). Significant values appear in *italic*.

local vulnerability traits	covariate	χ^2	slope	s.e.	<i>p</i>
thorax size	latitude	<i>66.51</i>	<i>-0.001</i>	<i>0.0001</i>	<i><0.001</i>
	elevation	15.55	-6.00×10^{-6}	1.00×10^{-6}	<i><0.001</i>
thermal tolerance	latitude	<i>390.1</i>	<i>0.004</i>	<i>0.0002</i>	<i><0.001</i>
	elevation	12.63	7.00×10^{-6}	2.00×10^{-6}	<i><0.001</i>
breeding habitat	latitude	59.75	<i>-0.003</i>	<i>0.0004</i>	<i><0.001</i>
	elevation	1.42	-6.00×10^{-6}	5.00×10^{-6}	0.23
extinction risk index	latitude	<i>719.99</i>	<i>-0.01</i>	<i>0.0003</i>	<i><0.001</i>
	elevation	43.93	-3.00×10^{-5}	5.00×10^{-6}	<i><0.001</i>

4. Discussion

As expected, we found that a greater regional extinction risk is generally associated with narrower thermal limits and breeding in lotic systems, but counter to expectations, did not correspond with smaller body size and even emerged as positively related in Zygoptera. The relationship between extinction risk and thermal tolerance in zygopterans makes sense as species of this suborder tolerate a wider environmental temperature range than anisopterans [60]. Previous works have pointed out that GRS of odonates is related to climate [61], thus cold-adapted odonate species are poised to 'lose' first in a warming climate situation [62]. Of course, insect relations with climate are more complex. Actually, the evolutionary patterns of odonate thermoregulation are driven by interactions with biogeographic origin, body size, surface colour and behaviour, at both local and broad scale, across temperate and tropical regions [60,63,64]. Still, a general pattern is that larger odonate species tend to be endothermic or heliothermic, whereas smaller species tend to be more ectothermic [60]. These relationships between body size and thermoregulation could explain the difference in extinction risk and thermal tolerance across suborders, where anisopteran GRS is less associated to climate compared to zygopteran GRS because of broader thermal limits in the latter suborder. It may also explain the contrasting size and thermal correlations with extinction risk observed in Zygoptera but not in Anisoptera (figure 1).

We found that lotic breeders of both suborders tend to have a more limited GRS and higher extinction risk than lentic species. In relation to this, Powney *et al.* [55] concluded that the degree of habitat specialization and GRS were key traits associated with the occurrence trends for Odonata. At a higher taxonomic level than only odonates, it has been suggested that the higher persistence of metapopulations, together with their smaller geographical ranges and reduced gene flow, may favour the evolutionary specialization of lotic macroinvertebrate species [65]. The relatively short-cycle hydroperiod of lentic habitats has selected for higher colonization capacities in standing-water species compared with their lotic relatives [27]. Thus, our results concur with previous analyses in other odonate species. For example, the stronger dispersal propensity of lentic odonates may have enabled a faster post-glacial recolonization of suitable regions, resulting in larger GRS [28]. Possibly, such dispersal propensity served as a mechanism for lentic odonates to better track changes in their climatic niche and thus avoid dry phases [64,66]. This may have ultimately conferred lentic odonates a lower extinction risk compared to lotic odonates.

Body size, understood as thorax length, did not relate to GRS and, consequently, extinction risk in Anisoptera, possibly due to the wide range of sizes across the 400 species we examined. Conversely, size positively covaried with the GRS of Zygoptera, so that larger damselflies may face higher viability costs and sexual selection pressures that make them more prone to extinction [67]. There are some ecological and functional issues related to this size metric that are worth discussing. On one hand, thorax size is positively related to dispersal ability [37], which may explain why it is a conserved trait across Odonata [50] and clarifies why anisopterans have a higher dispersal ability [64,68] and are adapted to different habitats than zygopterans [66]. A higher propensity to disperse and colonize would result in a larger GRS and lower extinction risk in North America for most anisopteran

species [69]. On the other hand, size is also related to thermal tolerance in ectotherms, and in this regard, larger-bodied species may be more susceptible to critical thermal maxima (CT_{max}) by oxygen limitation because of their lower surface area to volume ratio [70]. The nature of this ratio would constrain the odonate capacity to extract oxygen from their environment. Still, these mechanisms cannot explain the wide size distribution of North American odonates.

Our results indicate a general trend for larger anisopterans and smaller zygopterans occurring with decreasing latitude. Growing evidence suggests that body size of ectotherms tends to be smaller at lower latitude, otherwise known as Bergmann's rule [21], which is consistent with the pattern found for Zygoptera. However, odonates may show nonlinear size clines with latitude due to shifts in voltinism and biotic factors such as prey availability and size distribution [71]. Of course, there is not a unique mechanism that explains all patterns for both suborders and at least two explanations can be put forward. First, extirpation patterns for zygopterans are possibly explained by their low reproductive rates in colder environments. In this sense, natural selection would favour a larger body size to enhance fecundity at each reproductive episode [72]. Second, extirpation patterns for anisopterans might be explained by the metabolic cold adaptation hypothesis [73]: the faster larval growth at a higher temperature would result in a larger size at emergence [72,74]. The resulting balance and/or operation of both mechanisms should be studied.

We also found that species of both suborders tended to be more climatic tolerant at Southern regions (subtropical or warm-temperate Mexico and US) than at Northern regions (cold temperate or boreal US and Canada). This is in line with a simulation and experimental study of Zygoptera [33], and similar results have been described for other ectotherms [75]. Climatic niche conservatism may account for the extirpation risk of odonate species along the latitudinal gradient in North America. Also, our results suggest that thermal tolerance varies across the geography of North America [73]. This means that a biogeographical origin and, thus, the history of the region may regulate local vulnerability and current species distribution [63,76,77]. For instance, the Mexican Transition Zone that consists of five biogeographic provinces, mostly mountain ranges, and at least four cenocrons (i.e. sets of taxa that share the same biogeographical history, biotic origin, and evolutionary history) [78] have probably rendered a complex mixture of odonate biotas [79]. Thus, the dramatic thermal fluctuations associated with Mexican mountain ranges may have selected for thermal-generalist species. On the contrary, the boreal and temperate Northern regions are home to many cold-adapted and thermal-specialist species which are, however, more vulnerable to local extirpation [33,63].

For both suborders, thermal tolerances and extinction risk were associated with elevation ranges. Based on our results, Odonata species at lower elevation in tropical latitude are the most vulnerable to extinction, but they are also relatively tolerant to extirpation by climatic changes. Similar results were found by Colwell *et al.* [80], who suggested that a high proportion of tropical species would not be adapted to temperatures projected across elevational ranges under warming scenarios. Moreover, evidence suggests that ectotherms can more readily acclimate and thus adapt to colder temperatures than to warmer temperatures [26], which in turn suggests that species are more likely to persist at higher elevations albeit with reduced extents and areas of occurrence [81].

Under a global warming scenario, we suggest that odonate species at lower elevations in tropical latitudes are unlikely to be extirpated. Instead, odonate species from the plains at higher latitudes could be the most vulnerable to extirpation. This is because lower elevations are already warm in the tropics and thus naturally buffered against further warming, whereas species adapted to cooler higher elevations would be more susceptible to warming [82]. More generally, our analysis indicates that the extinction risk of Odonata varies along latitudinal and elevational gradients.

It is important to consider extinction risk at regional and local (extirpation) scales when defining the priorities of conservation [83]. From our analysis, we can identify two priority areas for Odonata conservation in North America. One is the cold temperate to sub-boreal northeastern USA. This is a centre of Nearctic species richness and complex biogeographical and evolutionary heritage [63,79] that includes a high percentage of regionally imperiled and locally vulnerable species [18]. Coastal New England, for example, contains several regional endemic species with strong habitat specialization [84,85]. Another priority area is the transversal neo-volcanic system, a centre of diversity and endemism deriving from multiple biogeographic origins [79]. Our maps suggest this area, at the transition of the Neotropical and Nearctic biogeographic realms, may contain the highest number of Odonata species prone to regional extinction, and some of these species extend into the southern USA, helping to create the concentrations of biodiversity including many at-risk species [85–87].

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Data accessibility. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.bk3j9kd79> [93].

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