LARGE SCALE PATTERNS OF AFRICAN AND EUROPEAN ODONATA; THE IMPORTANCE OF FUNCTIONAL TRAITS

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SUMMARY

Biodiversity patterns, community composition, and ecological dynamics are linked to species' responses to climatic conditions, biotic interactions, and dispersal limitations. Climate change has led to shifts in species ranges to higher altitudes and latitudes, changes in species population trends, and changes in species phenology. That makes climate change a fundamental concern for biodiversity conservation and makes understanding the effect of climate change on biodiversity a central theme in ecology. A promising approach to understanding the mechanisms shaping species distribution and community composition is linking physiological processes, functional traits, and the climatic environment.

Two ubiquitous features of animals of great functional importance are body size and body colour. For instance, both traits influence the temperature excess of species and thereby have significant consequences on species distributions, abundances, activities, and development. However, thus far, support for the importance of body size and body colour is sparse for insects, particularly at larger spatial and taxonomic scales. In addition, the effects of both traits on community composition and species' responses to environmental changes remain poorly understood.

Whereas it is difficult to monitor species populations across entire ranges, the IUCN established criteria that allow taxon experts to broadly categorize the threat status of species. However, only 1 % of the insects described so far have been assessed, with 26 % of these categorised as data deficient. Especially in tropical regions and for tropical taxa, we lack an understanding of the drivers associated with threatened insect species.

The overall objective of this PhD thesis was to investigate the importance of interactions between environmental factors and species' functional traits across Europe and Africa. My work focused on damsel- and dragonflies (Odonata) because of their ecological importance and exceptional natural history record among insects. With this, I aim to improve

our understanding of the mechanistic processes underlying biogeographical patterns and species extinction risk and ultimately improve forecast of the ecological consequences of climate change.

In one chapter of this thesis, I quantified the colour lightness and body volume of European Odonates and combined these traits with survey data for local assemblages across Europe. Based on this continent-wide yet spatially explicit dataset, I tested for effects of temperature and precipitation on the colour lightness and body volume of local assemblages and assessed differences in their relative importance and strength between lentic and lotic assemblages. I show that the colour lightness of assemblages of odonates increased, and body size decreased with increasing temperature. My results demonstrate that the mechanisms underlying colour lightness and body size variations scale to local assemblages. Together with previous studies on larger spatial scales, these results underline the general importance of colour- and size-based thermoregulation in insects. Both size- and colour-based thermoregualtion were of similar importance for species preferring lentic and lotic habitats (standing vs. running water), but the higher dispersal ability of lentic species seems to allow them to better track their thermal optimum.

In another chapter, I integrated trait-based models with environmental factors to investigate the mechanistic underpinnings of species' extinction risk for 489 African and European Odonates. Using body size, wing load, and habitat preference, I incorporate current theoretical and empirical support for single effects of environmental variables on species traits into structural ecological models. Specifically, I tested whether species are generally larger in colder environments; whether species adapted to less stable habitats and with lower wing loads have smaller ranges; and finally, the extent to which these trait-environment relationships translate into a higher extinction risk of species. The results of this chapter demonstrate that species adapted to lotic habitats as well as smaller species and species with

high wing loads have smaller range sizes. In addition, larger species and those with lower wing loads had more northern distributions and inhabited colder climates. Species with smaller ranges and those occurring in colder and more northern regions had a higher extinction risk. I thereby demonstrate that strong links between intrinsic traits (body size, wing load, and habitat preference) and extrinsic traits (range size, thermal preference, and latitudinal position) can explain a substantial part of the variation in species' extinction risk. However, in contrast to models of extrinsic traits alone, I emphasize that the mechanisms underpinning species' extinction risk are important to consider for understanding which species are particularly threatened and why. Thereby, trait-based models have a high potential to forecast and mitigate the negative impacts of environmental changes and other threats to species.

In another chapter, I investigated the potential of Odonates as biological control predators of mosquito larvae under almost natural conditions. I found that the widespread dragonfly *Bradinopyga strachani* is capable of breeding in and naturally colonising water storage containers used in typical rural homes, which are breeding grounds for mosquitoes. My mesocosm experiments show that the presence of *B. strachani* resulted in a drastic reduction of mosquito larvae density, especially in sunlit containers. My results confirm that dragonfly larvae are effective biological control agents of the disease-causing vector, with great benefits to the livelihood of people.

In summary, I demonstrate the importance of the mechanistic links between colour lightness and body size with the temperature regime which shapes the biogeographical patterns of European Odonates using spatially explicit survey data. The consistency of this reiterates the general importance of thermal melanism and Bergmann's rule for ectotherms at the local assemblage scale. However, besides highlighting the essential role of traits involved in thermoregulation in shaping the distribution of Odonates, the greater dispersal ability of

lentic species in combination with the climatic history seems to have allowed them to better cope with the historical climatic changes. Furthermore, my results highlight the importance of functional traits in species extinction risk assessments. Body size, habitat preference, and wing load explain why some species are particularly threatened and may thus serve as a red flag for threat assessment in conservation, even for species that lack distribution data. These integrative trait-based analyses are particularly relevant for providing links between ecology and conservation, which are important for completing and predicting species threats.

These results underline the ecological importance of Odonates and highlight a great potential for integrating interactions of morphological traits with species phylogenetic data and proxies of dispersal ability, into trait-based models to improve our understanding of biological responses to environmental changes and other potential threats. The importance of the functional traits of species and the generality of their impact on ecological dynamics stress that mobilization of trait data provides an important future avenue to improve baseline predictions and the information basis for large scale conservation of insect diversity.

ZUSAMMENFASSUNG

Biodiversitätsmuster, die Zusammensetzung von Artengemeinschaften und ökologische Dynamiken hängen mit den Reaktionen der Arten auf klimatische Bedingungen, biotische Wechselwirkungen und Ausbreitungsbeschränkungen zusammen. Der Klimawandel hat zu Verschiebungen der Verbreitungsgebiete von Arten in höhere Höhen und Breiten und zu Veränderungen in der Populationsentwicklung und in der Phänologie von Arten geführt. Dies macht den Klimawandel zu einem grundlegenden Anliegen für den Schutz der Biodiversität und macht das Verständnis der Auswirkungen des Klimawandels auf die Biodiversität zu einem zentralen Thema in Ökologie. Ein vielversprechender Ansatz zum Verständnis der Mechanismen, die die Artenverteilung und die Zusammensetzung der Gemeinschaft prägen, ist die Verknüpfung von physiologischen Prozessen, funktionellen Merkmalen und der klimatischen Umgebung.

Zwei allgegenwärtige Merkmale von Tieren von großer funktioneller Bedeutung sind deren Körpergröße und Körperfarbe. Beide Merkmale beeinflussen beispielsweise den Temperaturüberschuss von Arten und haben dadurch erhebliche Auswirkungen auf die Verbreitung, Häufigkeit, Aktivität und Entwicklung von Arten. Bisher ist die Bedeutung der Körpergröße und Körperfarbe für Insekten jedoch spärlich untersucht, insbesondere auf größeren räumlichen und taxonomischen Skalen. Darüber hinaus sind die Auswirkungen beider Merkmale auf die Zusammensetzung der Gemeinschaft und die Reaktionen der Arten auf Umweltveränderungen nach wie vor kaum bekannt.

Während es schwierig ist, Populationen über ganze Verbreitungsgebiete hinweg zu beobachten, hat die IUCN Kriterien festgelegt, die es Taxonexperten ermöglichen, den Bedrohungsstatus von Arten allgemein zu kategorisieren. Allerdings wurden bisher nur 1 % der beschriebenen Insekten bewertet, von denen die Datengrundlage bei 26 % als unzureichend eingestuft wurden. Insbesondere in tropischen Regionen und für tropische Taxa

fehlt uns das Verständnis der Treiber, die mit bedrohten Insektenarten verbunden sind. Das übergeordnete Ziel dieser Doktorarbeit war es, die Bedeutung von Wechselwirkungen zwischen Umweltfaktoren und funktionellen Merkmalen von Arten in Europa und Afrika zu untersuchen. Meine Arbeit konzentrierte sich auf Libellen (Odonata) aufgrund ihrer ökologischen Bedeutung und außergewöhnlichen naturgeschichtlichen Aufzeichnungen unter den Insekten. Damit möchte ich unser Verständnis der mechanistischen Prozesse verbessern, die biogeografischen Mustern und dem Artensterbenrisiko zugrunde liegen, und letztendlich unsere Prognosen der ökologischen Folgen des Klimawandels verbessern.

In einem Kapitel dieser Arbeit habe ich die Farbhelligkeit und das Körpervolumen europäischer Odonaten quantifiziert und diese Merkmale mit Erhebungsdaten für lokale Populationen in ganz Europa kombiniert. Basierend auf diesem kontinentweiten, aber räumlich expliziten Datensatz habe ich die Auswirkungen von Temperatur und Niederschlag auf die Farbhelligkeit und das Körpervolumen lokaler Artengemeinschaften getestet und Unterschiede in ihrer relativen Bedeutung und Stärke zwischen lentischen und lotischen Arten bewertet. Ich zeige, dass mit steigender Temperatur die Farbhelligkeit von Ansammlungen von Odonaten zunimmt und die Körpergröße abnimmt. Meine Ergebnisse veranschaulichen, dass die Mechanismen, die der Farbhelligkeit und den Variationen der Körpergröße zugrunde liegen, auf lokale Ansammlungen skalieren. Zusammen mit früheren Studien auf größeren räumlichen Skalen zeigten die Ergebnisse die allgemeine Bedeutung der farb- und größenbasierten Thermoregulation bei Insekten. Diese Mechanismen waren von ähnlicher Bedeutung für Arten, die lentische und lotische Lebensräume bevorzugen (stehendes vs. fließendes Wasser), aber die höhere Ausbreitungsfähigkeit lentischer Arten scheint es ihnen zu ermöglichen, ihr thermisches Optimum besser zu verfolgen.

In einem anderen Kapitel habe ich merkmalsbasierte Modelle mit Umweltfaktoren integriert, um die mechanistischen Grundlagen des Artensterbenrisikos für 489 afrikanische und europäische Odonaten zu untersuchen. Unter Verwendung von Körpergröße, Flügelbelastung und Lebensraumpräferenz integrierte ich aktuelle theoretische und empirische Unterstützung für einzelne Auswirkungen von Umweltvariablen auf Artenmerkmale in strukturelle ökologische Modelle. Insbesondere habe ich getestet, ob Arten in kälteren Umgebungen im Allgemeinen größer sind, ob Arten, die an weniger stabile Lebensräume angepasst sind und geringere Flächenbelastungen aufweisen, kleinere Verbreitungsgebiete haben und schließlich das Ausmaß, in dem diese Merkmal-Umwelt-Beziehungen zu einem höheren Aussterberisiko von Arten führen. Die Ergebnisse dieses Kapitels zeigen, dass Arten, die an lotische Lebensräume angepasst sind, sowie kleinere Arten und Arten mit hohen Flügelbelastungen kleinere Verbreitungsgebiete haben. Darüber hinaus hatten größeren Arten und solche mit geringerer Flügelbelastung eine nördlichere Verbreitung und bewohnten kältere Klimazonen. Arten mit kleineren Verbreitungsgebieten und solche, die in kälteren und nördlicheren Regionen vorkommen, hatten ein höheres Aussterberisiko. Ich zeige damit, dass starke Verbindungen zwischen intrinsischen Merkmalen (Körpergröße, Flügelbelastung und Lebensraumpräferenz) und extrinsischen Merkmalen (Verbreitungsgebietsgröße, thermale Präferenz und Breitengradposition) einen wesentlichen Teil der Variation des Artensterbenrisikos erklären können. Im Gegensatz zu Modellen von extrinsischen Merkmale allein hebe ich jedoch hervor, dass es wichtig ist, die Mechanismen zu berücksichtigen, die dem Aussterberisiko von Arten zugrunde liegen, um zu verstehen, welche Arten besonders bedroht sind und warum. Daher haben merkmalsbasierte Modelle ein hohes Potenzial, die negativen Auswirkungen von Umweltveränderungen und anderen Bedrohungen für Arten vorherzusagen und abzumildern.

In einem anderen Kapitel habe ich das Potenzial von Odonaten bei der biologischen Bekämpfung von Mückenlarven unter nahezu natürlichen Bedingungen untersucht. Ich fand heraus, dass die weit verbreitete Libelle *Bradinopyga strachani* in der Lage ist, sich in

Wasserspeicherbehältern, die in typischen ländlichen Häusern verwendet werden und Brutstätten für Moskitos sind, zu vermehren und diese auf natürliche Weise zu besiedeln. Meine Mesokosmosexperimente zeigen, dass das Vorhandensein von *B. strachani* zu einer drastischen Verringerung der Mückenlarvendichte führte, insbesondere in sonnenbeschienenen Behältern. Meine Ergebnisse bestätigen, dass die Libellenlarven wirksame biologische Kontrollmittel des Krankheitsüberträgers sind, mit großen Vorteilen für die Lebensgrundlage der Menschen.

Zusammenfassend demonstriere ich die Bedeutung der mechanistischen Zusammenhänge zwischen Farbhelligkeit und Körpergröße mit dem Temperaturregime, das die biogeografischen Muster europäischer Odonaten prägt, indem ich räumlich explizite Erhebungsdaten verwende. Die Allgemeingültigkeit dieser Beziehungen bekräftigt die allgemeine Bedeutung des thermalen Melanismus und der Bergmannschen Regel für Ektothermen auf der Skale lokaler Artengemeinschaten. Abgesehen von der Hervorhebung der wesentlichen Rolle von Merkmalen, die an der Thermoregulation beteiligt sind, bei der Gestaltung der Verteilung von Libellen, scheint die größere Ausbreitungsfähigkeit lentischer Arten in Kombination mit der Klimageschichte es ihnen ermöglicht zu haben, die historischen Klimaänderungen besser zu bewältigen. Darüber hinaus unterstreichen meine Ergebnisse die Bedeutung von funktionalen Merkmalen bei der Risikobewertung von Artensterben. Körpergröße, Lebensraumpräferenz und Flügelbelastung erklären, warum einige Arten besonders bedroht sind, und können daher bei der Bedrohungsbewertung im Naturschutz als Warnsignal dienen, selbst für Arten, für die keine Verbreitungsdaten vorliegen. Diese integrativen merkmalsbasierten Analysen sind besonders relevant, um Verbindungen zwischen Ökologie und Naturschutz herzustellen, die wichtig für die Vervollständigung und Vorhersage von Artenbedrohungen sind.

Diese Ergebnisse heben die ökologische Bedeutung von Libellen hervor und unterstreichen das große Potenzial für die Integration von Wechselwirkungen morphologischer Merkmalen mit phylogenetischen Daten, und Näherungswerten der Ausbreitungsfähigkeit in merkmalsbasierte Modelle, um unser Verständnis biologischer Reaktionen auf Umweltveränderungen und andere potenzielle Bedrohungen zu verbessern. Die Bedeutung der funktionellen Merkmale von Arten und die Allgemeingültigkeit ihres Einflusses auf die ökologische Dynamik unterstreichen, dass die Mobilisierung von Merkmalsdaten eine wichtige zukünftige Möglichkeit zur Verbesserung von Basisvorhersagen und der Informationsgrundlage für die Erhaltung der Insektenvielfalt auf großen Skalen darstellt.

PART I – INTRODUCTION

CHAPTER ONE

1.0 General background

Biodiversity patterns, community composition, and ecological dynamics are linked to species' responses to climatic conditions, biotic interactions, and dispersal limitations (Ricklefs, 2004). Climate change has led to shifts in species ranges to higher altitudes and latitudes, changes in species population trends, and changes in species phenology (eg., Hickling et al., 2005; Braune et al., 2008; Bowler et al., 2021). That makes climate change a fundamental concern for all biodiversity. However, not all species can fully track climatic changes or compensate for them through plasticity (Buckley & Kingsolver, 2012). A promising approach to understanding the mechanisms shaping species distribution and community composition is by linking physiological processes, functional traits, and the climatic environment (Chown and Gaston, 1999; Chown et al., 2004; Violle et al., 2007).

Gloger's rule, for instance, relates body pigmentation to the humidity of the environment such that within related endotherms, darker forms occur in warm and humid regions (Gloger, 1833). According to Bergmann's rules, the body size of endotherms increases with decreasing environmental temperature due to the thermoregulatory advantage of a lower surface-to-volume ratio of large-sized species, supporting heat retention (Bergmann, 1848). According to the thermal melanism hypothesis, darker ectotherms are at an advantage in cool regions because of color-based heat gain, and lighter ectotherms in warm regions because they reflect more solar radiation (Clusella Trullas et al., 2007).

Whereas it is difficult to monitor species populations in detail and across entire ranges, the International Union for the Conservation of Nature (IUCN) established criteria that allow taxon experts to broadly categorize the threat status of species ranging from not evaluated through vulnerable to extinct. These threat categories are mainly determined by assessments of the contemporary extent of occurrence and occupancy of species because the availability of time-series data is typically sparse and lacking for rare and highly threatened species (Jeliazkov et al., 2022; Red List Guidelines from IUCN Standards and Petitions Subcommittee, 2022). The IUCN threat status assessments thereby provide important baseline information for the prioritization of conservation efforts for species and taxa. Although the understanding of underlying causes of species extinction is essential for mitigating the impacts of climate change, why some species are more threatened than others remains poorly understood.

1.1 Effect of Climate change on biodiversity

Climate change influences the conditions in which organisms develop in both aquatic and terrestrial environments. This causes species to respond in several ways including change in their phenology (Parmesan, 2006; Braune et al., 2008; Dingemanse & Kalkman, 2008; Powney et al., 2015; McCauley et al., 2018; Bowler et al., 2020), and morphological traits (see Gardener et al., 2011), which may affect population dynamics, distribution, and persistence. Climate change is one of the main factors responsible for the increased habitat change and biodiversity loss. The general pattern of decreasing species richness from South to North (latitudinal gradient; south-west to north-east in Europe) has been found in many taxa and this correlates with several factors (e.g., Hassall et al., 2011; Pinkert et al., 2018, Pinkert et al, 2020b). For instance, the distribution of European Odonates have been shown to be modified largely due to climate change (e.g., Termaat et al., 2019) with more species range-expansion than contractions especially towards the geographic poles (Braune et al., 2008; Cerini et al., 2020; Grewe et al., 2013; Hickling et al., 2005). These shifts have been demonstrated more in warm adapted species (Termaat et al., 2019; Bowler et al., 2021; Assandri, 2021) and lentic species (Cerini et al., 2020; Assandri, 2021).

As powerful flyers especially dragonflies capable of covering long distances, they are able to colonize new areas when the immediate environment becomes unfavourable (Shiffer and White, 2014). The stability and permanence of freshwater habitats are known to affect the speciation and migration of species (Southwood, 1962; Ribera et al., 2001; May, 2019). Lentic (standing) and lotic (flowing) habitats present species with unique characteristics as they differ in their environmental and spatio-temporal properties with lentic habitats being comparatively younger, less stable, and less predictable than lotic habitats (Ribera et al., 2001; Ribera and Vogler, 2000; Williams, 2006; Rosset et al., 2017). Similarly, the hydrological connectivity of each habitat type contributes to its stability, hence, whereas lotic species can cope with climatic changes by moving up or down the same river, lentic species may have to fly several kilometres to find a suitable habitat once their habitat, for instance, a lake or pond dries out. For that matter, species in lentic habitats tend to have larger geographic ranges than lotic species (Ribera and Vogler, 2000; Arribas et al., 2012; Grewe et al., 2013). Lotic species have higher species turnover with richness declining towards the poles while the proportion of lentic species increases with latitude (Hof et al., 2006; Pinkert et al., 2018). Dispersal ability rather than the ecological tolerance of lotic species have been suggested to account for these variations in range size and richness between lentic and lotic species (e.g., Arribas et al., 2012), and this is associated with the ability of lentic species to disperse more readily into suitable habitats made available by a warming climate. In addition to dispersal ability, body size, abundance, and niche breadth are related to range size (Gaston, 2003).

Several traits studied as proxies of dispersal ability including wing size, body size, and flight muscles (e.g., McCauley, 2010, 2013; McCauley et al., 2014; Schilder and Marden, 2004) have assumed that dispersal patterns are only driven by the dispersal ability of species.

Aside dispersal ability varying with habitat preference, many other ecological and evolutionary processes influences species distribution and abundance (e.g., Kearney and Porter, 2009). For instance, the differences in energy allocation strategies and mobility cost among species mediates the effects of morphological traits (eg., Pinkert et al., 2020a). Species might, for instance, compensate an investment into body size or melanin production, by allocating less energy to growth, maintenance, or mobility (Boggs and Freeman, 2005; Boggs 2009).

With reports of insect decline worldwide, there is the need to understand mechanisms and identify ecological traits such as larval specificity, habitat preference, overwintering stage, length of flight period, body size, and wing span that contribute or predict insect extinction risks (Mattila et al., 2008; Terzopoulou et al., 2015; Rocha-Ortega et al., 2020). Also, because ecological traits that are correlated with extinction risk may be different from those correlated with distribution change (Mattila et al., 2006), there is the need to properly understand the physiological mechanisms underlying variations in species distribution, abundance, and extinction risk. Hence, it is important to include functional traits in species distribution models (e.g., Kearney and Porter, 2009) and extinction risk assessments.

1.2 Conservation of Odonates

There are currently about 6373 described dragonflies and damselflies worldwide as opposed to the estimated 7000 (Kalkman et al., 2018; Paulson et al., 2022). Genetic analyses have eased the identification and resolution of known Odonates and new species (e.g., Mens et al., 2016; Dijkstra et al., 2015). The Odonata Barcode Initiative for instance, has generated about 16,979 COI sequences of 1,983 species worldwide (BOLD, www.boldsystems.org, accessed November 13, 2021). While some authors have hinted at challenges with insect identification using DNA barcoding (Rewicz et al., 2020; Ferreira et al., 2017), the milestone achieved with

DNA-based methods of species identification serves as a basis for rapid and reliable species identification. For instance, 400 new species were described between 2006 and 2016 (Dijkstra et al., 2013; Dijkstra et al., 2015; Kippings et al., 2017). At this rate, Dijkstra et al. (2013) opine that about 95 % of Odonates could be described by 2030.

Currently, 6,016 species of dragonfly and damselfly have been assessed and published by the IUCN (www.iucnredlist.org; accessed January 6, 2022). This makes them the most accessed insect taxa. Across the European continent, 143 dragonflies and damselflies have been described (Kalkman et al., 2018). The threat statuses of 137 European species have been assessed according to the IUCN database (www.iucnredlist.org; accessed November 6, 2021). Sixteen species have been categorized as threatened (Endangered – 5, Vulnerable – 4, and Near threatened – 7). There is a high public appeal of dragonflies and damselflies in Europe evident in the high amount of data from citizen scientists (Boudot and Kalkman, 2015; Bowler et al., 2021). The availability of numerous field guides and distribution atlases (e.g., Boudot and Kalkman, 2015; Dijkstra and Lewington, 2006; Dijkstra et al., 2020) is one of the major reasons for the ease of involvement of Citizen Scientists.

The threat status of 891 Odonates in Sub-Saharan Africa have been assessed (www.iucnredlist.org; accessed November 6, 2021) with about 13 % of these are considered threatened (Critically endangered – 17, Endangered – 36, Vulnerable – 28, Near Threatened – 30), and about 18 % considered as data deficient. Odonate diversity is highest in West and Central Africa, where 50 % are restricted to forests (Kalkman et al., 2008). West Africa homes about 311 Odonate species with nearly 20% endemic to the region (Dijkstra and Vick, 2004). The species composition, diversity, and speciation of dragonflies and damselflies in Africa are highly influenced by forests which harbour a diversity of aquatic habitats (Dijkstra and Clausnitzer, 2006). It has been suggested that over 10 % of known African Odonates require further attention (Dijkstra and Clausnitzer, 2006; Clausnitzer et al., 2012). Africa in the last two decades has made much effort to increase awareness of Odonates in the form of electronic databases (www.addo.adu.org.za) and field guides (Suhling & Martens, 2007; Samways, 2008; Dijkstra and Clausnitzer, 2014; Suhling et al., 2014; Tarboton & Tarboton, 2015, 2019).

Human-induced habitat modifications and destruction of freshwater systems, urban and agricultural expansion, and forest cover loss affecting water sources are some major threats facing dragonflies and damselflies. The IUCN outlines 10 major areas where Odonates are threatened with the biggest threats being agriculture and aquaculture, biological resource use, and pollution (www.iucnredlist.org; accessed November 6, 2021). According to the IUCN, the main conservation actions needed to protect Odonates involve land and water habitat protection and site management, habitat restoration, education, and awareness creation (www.iucnredlist.org; accessed November 6, 2021). With the majority of conservation strategies for threatened Odonates designed to protect their aquatic habitats (Dolný et al., 2014), other studies focussing on the impact of abiotic habitat changes have shown that the associated terrestrial environment also affect the diversity and abundance of Odonates (e.g. Hykel et al., 2016).

1.3 Importance of Odonates

Odonates play an important role in the food web of aquatic and terrestrial habitats. As larvae, they serve as prey to fish and amphibians and as predators to a variety of prey of different sizes. Adults are eaten by birds, bats, lizards, and spiders. Odonates have a rich phenotypic and ecological diversity in a single insect Order and hence are great model species for ecological and evolutionary studies such as sexual selection, behaviour, evolution of flight and life history (Córdoba-Aguilar, 2008). For these reasons, Odonates have been suggested to be a bridge between ecology and evolutionary genomics (Reviewed in Bybee et al., 2016).

Several organisms have been recognised as useful bioindicators of aquatic and wetland habitats (e.g., insects – Sahlén & Ekestubbe, 2001; Sánchez-Fernández et al. 2006; Lencioni, 2012; Roth et al., 2020; phytoplankton and algae – Hassan, 2020; Dixit et al., 1992; Omar, 2010; fish – Naigaga et al., 2011; Lopez-Lopez & Sedeno-Diaz, 2015). The practicality of collecting (sampling), sorting, and identifying dragonflies and damselflies makes them one of the best bioindicators of different habitat conditions and can provide information about the ecological state, biological health, and habitat diversity (Corbet, 1993). Dragonflies and damselflies meet the requirements for good bioindicators of wetlands and water quality because; (1) they are very sensitive to conditions at their breeding sites and surrounding terrestrial areas. They have a specific set of habitat requirements (Chovanec and Waringer, 2001; Schindler et al., 2003; Chovanec et al., 2014) and react to changes in the quality of the environment by dispersing as adults or even refusing to breed in the changed medium, (2) the taxonomy of dragonflies and damselflies is well known and the adults are easier to identify than many taxa (Oertli et al., 2005; Simaika & Samways, 2011; Chovanec et al., 2014; Kutcher and Bried, 2014), (3) their ecology, seasonality, and distribution are well known (especially in some geographic areas like Europe and North America), (4) they are economically cost-effective as it does not involve much capital to sample, collect, and identify them.

The sensitivity of Odonates to environmental change has resulted in their successful use as bioindicator taxa for selecting new areas for protection (Simaika and Samways, 2009; Clausnitzer et al., 2017), and for identifying important landscape characteristics (Raebel et al., 2012). Some African countries including South Africa have implemented the use of Dragonfly Biotic Index in freshwater monitoring (Samways & Simaika, 2016). Other Odonate indices include OHI – Odonata Habitat Index (Chovanec and Waringer, 2001); ORI – Odonata River Index (Golfieri et al., 2016); OCIC – Odonata Community Index – Corsica

(Berquier et al., 2016); and the DAI – Dragonfly Association Index (Chovanec et al., 2014). These indices however, are region-specific and would require revision of the parameters should it be transferred or applied in other regions (Sahlén and Ekestubbe, 2001; Clausnitzer, 2003).

1.4 Life history of Odonates

Since most of the lifespan is spent as an aquatic larva, site selection within the aquatic habitat is very important and has implications for resource partitioning, concealment from predators, prey detection, and the development of the larvae. Habitat conditions such as water depth, type of aquatic and edge vegetation, canopy and shade cover, the chemical properties of the water, rate of flow of water, water colour, water temperature, bank height, and many others affect the development of the larvae (Carchini et al., 2007; Goertzen and Suhling, 2013; Lambret et al., 2018). The aerial adult stage of the Odonates is important for dispersal, migration, and energy transfer across aquatic and terrestrial habitats and among trophic levels (Clarke et al., 1996; Gladyshev et al., 2011; Wikelski et al., 2006). It has been argued that, only the presence of exuviae and newly emerged adult (Tenerals) confirm that the individual developed successfully at the site (Chovanec and Waringer, 2001; Raebel et al., 2010). However, sampling adults, who may exhibit habitat specificity, is equally as effective as, and more advantageous than sampling of the earlier life stages (Bried et al., 2012; Samways and Simaika, 2016). This is because of the ease associated with identifying adults as compared to exuviae or larvae (seen in the number of available field guides based on adults compared to the immature life stages). On the contrary, the response of a particular stage to environmental changes may be dependent on the spatial scale of the assessment (Kietzka et al., 2021).

1.5 Aims of the present study

In this thesis, we aim to improve our understanding of the mechanistic links of functional traits with the temperature regime which shapes the biogeographical patterns of European and African Odonates and how the use of functional traits of Odonates can improve the predictions of species risk of extinction. We test if the trait-environment relationships reconcile with previous macroecological evidence of the mechanistic links of traits with the physiology and distribution of ectotherms using expert range maps. Specifically, we test 1) whether colour lightness of local assemblages in European Odonates increase with increasing temperature, 2) whether species are generally larger in colder environments, 3) whether these trait-environment relationships are more important for species adapted to less stable habitats, due to their greater dispersal propensity compared to those adapted to stable habitats, 4) whether species with a lower wing load as well as those adapted to less stable habitats have smaller ranges. Lastly, we assess the extent to which these trait-environment relationships translate into a higher extinction risk of species.

In addition, we assess the possibility of Odonates to colonise mosquito breeding habitats and reduce the mosquito population density in a field mesocosm experiment.

PART II – MANUSCRIPTS OF THIS THESIS

Outline

Large-scale patterns in functional traits of Odonates

The manuscripts presented in **Chapters II** highlights our support for previous macrophysiological (Pinkert et al., 2017; Zeuss et al., 2014, 2017) and experimental (May, 1991; Samejima & Tsubaki, 2010) studies, which suggest that temperature-driven colour lightness and body size variations strongly influence biogeographical patterns in ectotherms. We show that the predictions of the thermal melanism hypothesis and Bergmann's rule hold for local assemblage. That is, colour lightness of assemblages of European Odonates increase and body size decrease with increasing temperature. We disentangle the components of the traits and show that the trait-environment relationships in the average and phylogenetic predicted components were equally important for both lentic and lotic assemblages but were stronger in lentic assemblages when we account for the phylogenetic autocorrelation. The results highlight that the mechanism underlying colour lightness and body size variations are generally important. Owing to our contribution to understanding how species respond to climate, I have been invited to author a chapter in the second edition of *Dragonflies & Damselflies: Model Organisms for Ecological and Evolutionary Research*, where we present and discuss Odonata as a focal taxa for biological responses to climate change. In **Chapter III** we assess the mechanisms underpinning the links between functional traits and extinction risk of European and African Odonata and how extrinsic environmental traits modulate the relationship between intrinsic functional traits and Odonata risk of extinction. Specifically, we test, for the first time including the tropics, whether species are generally larger in colder environments. Secondly, we test whether species with a lower wing load as well as those adapted to less stable habitats have smaller ranges. Finally, we assess the extent to which these trait-environment relationships translate into a higher extinction risk of species. We do so by integrating current theoretical and empirical support for single effects among the considered variables into a generalized framework following the assumptions of trait-based theory. The results highlight that the ultimate cause of the effects of extrinsic traits on species' threat status are differences in species' dispersal ability, body size and habitat preference.

Odonates as biological control agents for mosquitoes

In Chapter IV, the importance of an Odonate species *Bradinopyga strachani* in biological control is demonstrated here when the species colonised water storage containers which served as breeding reservoirs for mosquitoes. Even though there are previous reports of the potential use of Odonates as predators for mosquitoes, most of these reports came from laboratory studies. To practicalize this, we created typical water storage containers used in rural homes and monitored the colonisation by mosquitoes and later *B. strachani* and how the mosquito larval density was reduced due to the presence of the predator. Insufficient engagement and communication with the public is an important limitation to successful biological control program as well as species conservation.

List of Manuscripts

Title: Temperature-driven colour lightness and body size variation scale to local assemblages of European dragonflies but are modified by propensity for dispersal.

Authors: **Daniel Acquah-Lamptey**, Martin Brändle, Roland Brandl**,** and Stefan Pinkert

Status: Published in *Ecology and Evolution*, 10: 8936–8948

Contribution: Data acquisition: 50 %, data analysis: 50 %, writing and revision: 70 %, concept: 20 %.

Title: Extrinsic environmental traits modulate the relationship between intrinsic functional traits and the extinction risk of European and African Odonata.

Authors: **Daniel Acquah-Lamptey**, Laura Maehn, Roland Brandl**,** Stefan Pinkert

Status: Manuscript in preparation

Contribution: Data acquisition: 50 %, data analysis: 60 %, writing and revision: 60 %, concept: 40 %.

Title: Effect of a dragonfly (*Bradinopyga strachani* Kirby, 1900) on the density of mosquito larvae in a field experiment using mesocosms.

Authors: **Daniel Acquah-Lamptey**, Roland Brandl

Status: Published in *Web Ecology*, 18, 81–89

Contibution: Data acquisition: 100 %, data analysis: 70 %, writing and revision: 80 %, concept: 90 %.

Other Manuscripts (Appendix)

Title: Odonata as focal taxa for biological responses to climate change

Authors: Stefan Pinkert, Viola Clausnitzer, **Daniel Acquah-Lamptey**, Paulo De Marco, Frank Johansson
Status: In press

Contribution: Total: 30 %

Title: Awareness of odonata (dragonflies and damselflies), an important insect order, among graduates in the Greater Accra region of Ghana

Authors: **Daniel Acquah-Lamptey**, Roman Fricke, Roland Brandl

Status: In preparation

Contribution: Data acquisition: 100 %, data analysis: 100 %, writing and revision: 90 %, concept: 90 %.

Title: Butterfly Diversity: An Indicator for Environmental Health within Tarkwa Gold Mine, Ghana.

Authors: Rosina Kyerematen, Samuel Adu-Acheampong, **Daniel Acquah-Lamptey**, Roger S. Anderson, Erasmus H. Owusu, Jones Mantey

Status: Published in *Environment and Natural Resources Research,* 8 (3).

Contribution: Data collection: 50 %, data analysis: 30 %, write up and revision: 30 %

Title: Using Orthoptera and Hymenoptera indicator groups as evidence of degradation in a mining concession (Tarkwa gold mine) in Ghana.

Authors: Rosina Kyerematen, Samuel Adu-Acheampong, **Daniel Acquah-Lamptey**, Roger S. Anderson

Status: Published in *International Journal of Tropical insect Science*, 40, 221-224

Contribution: Data collection: 50 %, write up and revision: 20 %

Title: Butterfly Assemblages of Two Wetlands: Response of Biodiversity to Different Environmental Stressors in Sierra Leone.

Authors: Rosina Kyerematen, Fatmata Kaiwa, **Daniel Acquah-Lamptey**, Samuel Adu-Acheampong, Roger S. Anderson

Status: Published in Open Journal of Ecology, 8, 379-395

Contribution: Data analysis: 40 %, write up and revision: 20 %

CHAPTER TWO

TEMPERATURE-DRIVEN COLOUR LIGHTNESS AND BODY SIZE VARIATION SCALE TO LOCAL ASSEMBLAGES OF EUROPEAN DRAGONFLIES BUT ARE MODIFIED BY PROPENSITY FOR DISPERSAL

Daniel Acquah-Lamptey, Martin Brändle, Roland Brandl**,** Stefan Pinkert

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2.1 ABSTRACT

Previous macrophysiological studies suggested that temperature-driven colour lightness and body size variations strongly influence biogeographical patterns in ectotherms. However, these trait–environment relationships scale to local assemblages and the extent to which they can be modified by dispersal remains largely unexplored. We test whether the predictions of the thermal melanism hypothesis and the Bergmann's rule hold for local assemblages. We also assess whether these trait–environment relationships are more important for species adapted to less stable (lentic) habitats, due to their greater dispersal propensity compared to those adapted to stable (lotic) habitats.

We quantified the colour lightness and body volume of 99 European dragon- and damselflies (Odonata) and combined these trait information with survey data for 518 local assemblages across Europe. Based on this continent-wide yet spatially explicit dataset, we tested for effects temperature and precipitation on the colour lightness and body volume of local assemblages and assessed differences in their relative importance and strength between lentic and lotic assemblages, while accounting for spatial and phylogenetic autocorrelation.

The colour lightness of assemblages of Odonates increased, and body size decreased with increasing temperature. Trait-environment relationships in the average and phylogenetic predicted component were equally important for assemblages of both habitat types but were stronger in lentic assemblages when accounting for phylogenetic autocorrelation.

Our results show that the mechanism underlying colour lightness and body size variations scale to local assemblages, indicating their general importance. These mechanisms were of equal evolutionary significance for lentic and lotic species, but higher dispersal ability seems to enable lentic species to cope better with historical climatic changes. The documented differences between lentic and lotic assemblages also highlight the *importance of integrating interactions of thermal adaptations with proxies of the dispersal ability of species into trait-based models, for improving our understanding of climate-driven biological responses.*

2.2 INTRODUCTION

Understanding the processes that shape species' distributions and the composition of assemblages is central to ecological research (Brown & Maurer, 1987; Cavender-Bares et al., 2009; McGill et al., 2006; Ricklefs, 2004). A straightforward approach to gain a process-based understanding is to investigate functional traits that link the physiology of a species with the ambient environment in which the species occurs (Chown et al., 2004; Violle et al., 2007). Ectothermic species must absorb thermal energy from their environment to be active and to maintain fundamental physiological processes, including growth and reproduction (Angilletta, 2009; Huey & Kingsolver, 1989). Therefore, ectotherms have evolved several behavioral (e.g., wing-whirring or basking; Corbet, 1980; May, 1979) and morphological adaptations to the climate in which they live (Angilletta, 2009; May, 1976).

Two of the most important morphological traits that influence the distribution of ectothermic organisms are probably their surface colour, particularly colour lightness (melanism), and body size. Fundamental physical principles link both traits to the heat gain and loss of an organism (Clusella-Trullas et al., 2007; Shelomi, 2012). On the one hand, melanization of the cuticle determines the absorption of solar radiation and hence heat gain, a mechanism referred to as thermal melanism (Clusella-Trullas et al., 2007; Gates, 1980; Kalmus, 1941). On the other hand, since an increase in body size implies a reduction of the surface area to volume ratio, larger bodies are able to retain heat more efficiently than smaller bodies (Shelomi, 2012). Besides thermoregulation, greater melanisation increases resistance against pathogens, by enhancing the structural integrity of cells (Gloger's rule, Rapoport, 1969; Wilson et al., 2001) and a larger body size is advantageous under dry conditions, as a lower surface area to volume ratio reduces water loss through the cuticle (Kühsel et al., 2017; Remmert, 1981).

While the colour lightness and body size of a species should reflect the climate in which it can live (Willmer & Unwin, 1981), the extent to which that species realizes the potential environmental niche depends on its dispersal. Important differences in a species' ability and propensity to disperse are related to the stability of their respective habitats (Southwood, 1977). In general, species restricted to spatially and temporally less stable habitats with higher dispersal abilities (Pellissier, 2015; Southwood, 1977) evolved set of adaptations (behavioral and morphological, Corbet, 1980) that facilitate persistence or the (re)colonization of habitats (Southwood, 1962), which are reflected in larger geographical ranges, stronger gene flow between populations and the ability to cope with climatic changes (Arribas et al., 2012; Hof et al., 2006; Marten et al., 2006; Pinkert et al., 2018). Freshwaters provide an ideal model system to test the predictions of this "habitat–stability–dispersal hypothesis" (Hof et al., 2012; Southwood, 1977). In the northern hemisphere, lentic water bodies (e.g., ditches and lakes) are ephemeral and date back to the Pleistocene, whereas the locations of rivers and streams (lotic waters) that carry water throughout the year have remained largely unaltered since the Mesozoic (Bohle, 1995 and sources therein). In contrast, though some lakes are very old (reviewed in Hutchinson, 1957), lotic habitats are on average more persistent over space and time than lentic habitats (Martens, 1997). Recent studies have shown that the ecological differences between species adapted to lentic and lotic habitats carry a phylogenetic signal (Letsch et al., 2016). Moreover, these differences have found to be associated with contrasting biogeographical and diversification patterns between the two groups (Abellán et al., 2009; Hof et al., 2008). For instance, Dehling et al. (2010) showed that the richness of lotic animals decreases from southern to northern Europe, whereas the richness of lentic animals is highest in central Europe. A broadly similar pattern has been reported for the richness of lentic and lotic Odonata (dragonflies and damselflies) on a global scale (Kalkman et al., 2008). Thus, in contrast to almost all other Odonata, the two youngest families (Coenagrionidae and Libellulidae; Rehn, 2003) that constitute the majority of lentic species globally (Kalkman et al., 2008) are disproportionally diverse in temperate climates. This suggests stronger trait–environment relationships in Odonates of lentic than lotic habitats due to the greater ability of the former to cope with past climatic changes (Arribas et al., 2012; Grewe et al., 2013; Pinkert et al., 2018). However, despite strong support for an impact of species' dispersal ability on biogeographical patterns, to what extent dispersal can modify trait–environment relationships remains largely unexplored.

Analyses of the large-scale patterns of interspecific variation in physiological traits offer a powerful approach to elucidate the general processes that shape biodiversity patterns (Chown et al., 2004). These macrophysiological inferences based on the assumption that the explanations for large-scale diversity patterns are found at lower levels of biological organization, as functional traits influence the fundamental physiological rates of individuals and populations whereas the consequences thereof play an important role in determining a species' fundamental niche (Gaston & Blackburn, 2000). On the one hand, previous physiological studies on few species (Brakefield & Willmer, 1985; Harris et al., 2013) and local scale studies (e.g., along elevational gradients) have reported strong links between physiological trait and the environment, but these are often limited in spatial extent (Brehm et al., 2018; Dufour et al., 2018; Peters et al., 2016; Xing et al., 2018). On the other hand, most of the studies conducted so far on the interspecific variation of colour lightness and body size in ectothermic species over large geographical ranges are based on expert range maps generated by interpolating species occurrence records across suitable habitats (e.g., Pinkert et al., 2017; Zeuss et al., 2014, 2017; but see Bishop et al., 2016). Hence, previous evidence of colour- and size-based thermoregulation has three important limitations. First, although at geographical scales expert range maps are generally considered to allow robust estimations of the full environmental range of species, the underlying distribution information tends to overestimate species' real distributional ranges (Hurlbert & Jetz, 2007; Merow et al., 2017). Second, the inherent spatial structure of expert range maps has been shown to inadvertently generate spurious spatial patterns for the richness and mean trait values of assemblages (Hawkins et al., 2017). Third, distribution data with a coarse resolution generate "synthetic" assemblages of species that do not necessarily form local assemblages. For instance, expert range maps typically also include records of populations that may no longer exist (or never existed) and pool species from different habitat types. Therefore, whether the previously documented relationships of colour lightness and body size with climate also scale to the local assemblage level remains largely unexplored.

In this study, we investigated trait–environment relationships using spatially explicit survey data for local assemblages of dragon- and damselflies (Odonata) across Europe. Specifically, according to the thermal melanism hypothesis and Bergmann's rule sensu *lato,* we expected (a) an increase in the colour lightness of local assemblages of Odonates with increasing temperature. If colour lightness and body size are also involved in pathogen resistance and desiccation tolerance, we expect that (b) local assemblages of Odonates are darker and smaller in more humid climates. In addition, given that adaptations to spatially and temporally less stable habitats allow lentic species to better cope with climatic changes (habitat–stability–dispersal hypothesis), we predicted that (c) the slopes of these relationships would be stronger for lentic than for lotic assemblages.

2.3 MATERIAL AND METHODS

2.3.1 Distribution data

Information on water body location and type (i.e. lentic or lotic) and the composition of local dragonfly communities across Europe were compiled from data obtained in an extensive literature search (Appendix 2.1). Only records of breeding species were included, to obtain species sets associated with the considered water bodies. Breeding records covered tandem pairs, ovipositing females, larvae, exuviae and recently emerged adults (Bried et al., 2015), resulting in 5,703 records of 99 dragonfly species and 524 local dragonfly communities across 28 European countries. After assemblages with less than three species were excluded (to obtain reliable estimates of assemblage means), the final dataset comprised of 518 local assemblages of dragonflies and damselflies (Fig. 2.1; 337 lentic, 181 lotic).

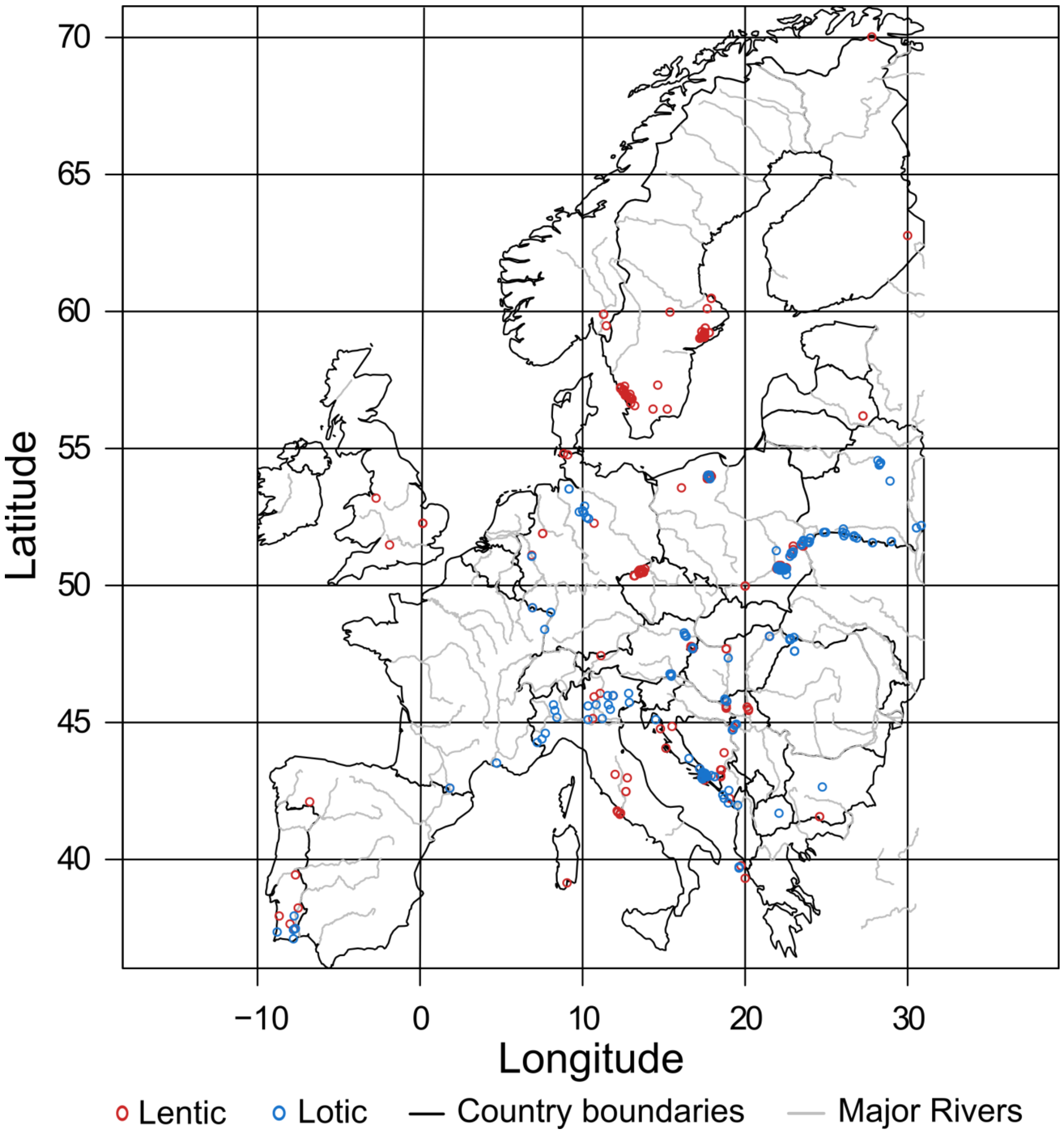

FIGURE | 2.1 Distribution of (lentic = 337, lotic = 181) assemblages of Odonates across Europe. Lentic assemblages are indicated with red circles, lotic assemblages with blue circles and the main European rivers in gray. The black outlines are country boundaries in the study region. The proportion of lotic habitats is higher in southern and central Europe. The space inside each circle represents the area for which the climate data were aggregated (a radius of ~1 km around the location of each community).

2.3.2 Trait data

Following the most common approach used in the analysis of morphological traits based on digital images (Pinkert et al., 2017; Zeuss et al., 2014, 2017), we calculated the average colour lightness and body volume of species using drawings of European Odonata (Dijkstra & Lewington, 2006). To prepare images for the analysis, the dragonfly body (head, abdomen and thorax) in scanned drawings of species' dorsal body surfaces (24-bits, sRGB, 1200 dpi resolution) was cropped out and saved to separate files using functions of Adobe Photoshop CS2. Based on these images, the average colour of the pixels of an image across the red, green, and blue channels was calculated as an estimate of the colour lightness of a species (8-bit gray values ranging from 0: absolute black to 255: pure white). In addition, these images were scaled with the magnification factor provided in Dijkstra and Lewington (2006) and used to calculate body volume in cm^3 ($\pi \times [½ \text{ length of pixel row}]^2 \times \text{pixel edge length}$) as an estimate of the body size of a species based on the assumption that Odonates generally have a cylindrical body form. The calculations were performed using functions of the R package *png* (Urbanek, 2013). Body volume instead of linear size measures, such as wing length, head width, and body length, was used because as a three-dimensional measure it allows for a more realistic estimate of the body mass of a species (Kühsel et al., 2017). Note that previous studies showed that the colour lightness and body volume estimates are correlated between drawings from different sources and between males and females (Pinkert et al., 2017; Zeuss et al., 2017). Subsequently, the average colour lightness and body volume were calculated across the species of each local assemblage.

2.3.3 Environmental data

Based on the predictions of the thermal melanism hypothesis and Bergmann's rule, we considered annual mean temperature as a predictor of geographical patterns in the colour lightness and body size of the assemblages of Odonates. In addition, annual precipitation (AP) was included as a predictor because of the protective function of melanin against pathogens under humid climates (e.g., Delhey, 2019; Rapoport, 1969; Stelbrink et al., 2019) and the hypothesised advantage of lower water loss in large insects under dry climates (Kühsel et al., 2017; Remmert, 1981). We considered only annual mean temperature and annual precipitation, rather than all 19 commonly used bioclimatic variables, to facilitate interpretations of their effects and comparability with other studies (e.g., Pinkert et al., 2017; Zeuss et al., 2017). Nevertheless, the two variables contributed strongly to the overall trends in temperature and precipitation from a principal component analysis based on the correlation of 19 commonly used bioclimatic variables (Table S2.1). Climate variables used in the analysis were extracted from climate data with a resolution of 2.5 arcminutes (retrieved from www.chelsa-climate.org; Karger et al., 2017, 2018), based on the geographical coordinates of the assemblages included in our analyses (with a buffer radius of approximately 1 km).

2.3.4 Statistical analyses

Previous studies found that the colour lightness and body size, as well as the habitat preference of European Odonates, carries a phylogenetic signal (Zeuss et al. 2014; Letsch et al., 2016; Pinkert et al., 2017). Based on a recent phylogeny of the European Odonates (Pinkert et al., 2018), we, therefore, partitioned the total variance of the colour lightness and body volume into a phylogenetic component and a species-specific component using Lynch's comparative method (Lynch, 1991), implemented in the R-package *ape* (Paradis et al., 2004). For data and methodology on the phylogeny of the European Odonates, see Pinkert et al. (2018). The phylogenetic component represents the variation in colour lightness and body volume predicted by the phylogenetic relationships of the species, whereas the species-specific component is the difference of the observed trait estimate from the phylogenetically predicted part. The advantage of this method is that it allows assessing the effect of phylogenetic signals in traits (i.e., P - component) that is often neglected as a source of bias, in addition to the model results that have been corrected for phylogenetic autocorrelation (i.e., S - component).

Tests for trait-environment relationships were performed using single and multiple ordinary least-squares regression models, with the average colour lightness and body size of Odonata assemblages as dependent variables and climatic variables as independent variables. Differences in the slopes of the relationships of colour lightness and body size with climatic variables between lentic and lotic habitats were determined by fitting interaction terms between the independent variables and habitat type. In all models, independent variables were scaled and centred (z-standardised) to facilitate their comparison. We checked mulitcollinearity among predictors, using the *vif* function of the R-package *car* (Table S2.2; Fox et al., 2016).

Since spatial autocorrelation in the survey data could violate the assumptions of our statistical models, i.e., that all data points are independent of each other, spatial correlograms of the model residuals were calculated using functions of the R-package *ncf* (Bjornstad, 2016). These correlograms indicated significant spatial autocorrelation in our data. Therefore, all analyses were repeated using spatial autoregressive error models (Dormann, 2007) that included a spatial distance weight according to the model-specific point of spatial independence (extracted from spatial correlograms shown in Figures S2.1-S2.2). All statistical analyses and calculations were conducted in R (version 3.5.1, R Core Team, 2016).

2.4 RESULTS

2.4.1 Trait-environment relationships

In all multiple regression models, the colour lightness of the assemblages of Odonates increased with increasing annual mean temperature and body volume decreased with increasing annual mean temperature (Table 2.1). In all multiple regression models, the colour lightness of the assemblages of Odonates was not affected by annual precipitation, but except for phylogenetically corrected models, body volume increased with increasing annual precipitation. These results were consistent with the results of single regression models (except that single regression of the average and phylogenetically predicted part of the variation in the colour lightness and annual mean temperature were not significant) and with the results of models that accounted for spatial autocorrelation (Table 2.1). The two climate predictors together explained up to between 20 % and 31 % of the variation in colour lightness and between 2 % and 4 % of the variation in body volume (Table 2.1, see Table S2.3 for regression models for individual habitat types).

TABLE | 2.1 Effect sizes (z-scores) and the explained variance of predictor variables from single and multiple regressions (r^2/R^2) of the average, phylogenetic and species-specific components of the average colour lightness and body volume of 518 assemblages of European Odonates with z-standardised temperature and precipitation variables. In addition, regression models (Nagelkerke pseudo-r^2/R^2) calculated with a spatial dependency weight are given. Significant relationships ($p < 0.05$) are shown in bold. The predictors are: annual mean temperature (AMT), and annual precipitation (AP). The P - component represents the phylogenetically predicted part of the respective trait and S - component represents the respective deviation of the average trait from the P - component.

				Average		S - component		P - component	
Model		Trait	Predictor	Z-score	r^2/R^2	Z-score	r^2/R^2	Z-score	r^2/R^2
Ordinary least-squares regression	Single	Colour lightness	AMT	**14.28**	0.28	**11.44**	0.20	**11.88**	0.22
			AP	**5.14**	0.05	**3.41**	0.02	**2.58**	0.01
		Body volume	AMT	–1.59	0.01	**–2.97**	0.02	–1.33	0.00
			AP	**2.25**	0.01	-0.25	0.00	**2.55**	0.01
	Multiple	Colour lightness	AMT	**13.12**	0.29	**10.80**	0.20	**11.55**	0.22
			AP	1.68		0.33		–0.74	
		Body volume	AMT	**–2.40**	0.02	**–3.04**	0.02	**–2.21**	0.02
			AP	**2.89**		0.68		**3.11**	
Spatial autoregressive error models	Single	Colour lightness	AMT	**11.62**	0.30	**9.87**	0.21	**10.73**	0.24
			AP	**2.69**	0.14	1.47	0.09	1.17	0.08
		Body volume	AMT	–1.77	0.03	**–2.50**	0.02	–1.60	0.03
			AP	**2.24**	0.03	0.77	0.01	**2.45**	0.03
	Multiple	Colour lightness	AMT	**11.32**	0.31	**9.57**	0.21	**10.64**	0.24
			AP	1.71		0.50		-0.06	
		Body volume	AMT	**–2.15**	0.04	**–2.59**	0.02	**–2.00**	0.04
			AP	**2.56**		1.04		**2.74**	

2.4.2 Differences in trait-environment relationships between habitat types

The relative importance of annual mean temperature and annual precipitation, as well as the slopes of the considered trait-environment relationships, differed between lentic and lotic assemblages (Figure 2.2). Among the 24 considered relationships (models of the two traits, corrected for phylogenetic and spatial autocorrelation), 6 were significant for both lentic and lotic assemblages, 6 were only significant for lentic and 5 were only significant for lotic assemblages (Table 2.2). The two groups mostly responded similarly to annual mean temperature and all the relationships that were only significant in lotic assemblages were responses to annual precipitation (see Table S2.4 for single regression models).

Except for one response of body size, the slopes of all relationships of climate variables with the average as well as the phylogenetically predicted part of the variation in the traits were similar in their strength between the two groups. By contrast, responses of the species-specific part of the variation in colour lightness and body size to climate were mostly stronger in lentic compared to lotic assemblages (Table 2.2). Similarly, the direction of the slopes of the relationships only differed between species-specific part of the variation in body size and annual precipitation for both ordinary least-squares regression and spatial autoregressive error models (Table 2.2).

TABLE | 2.2 Individual slopes and standard error of the predictor variables from multiple regressions (R^2) of the average, phylogenetic and species-specific components of the average colour lightness and body volume of (lentic = 337, lotic = 181) assemblages of European Odonates with z-standardised environmental variables. In addition, regression models (Nagelkerke pseudo-R^2) calculated with a spatial dependency weight are given. Shaded cells indicate significant differences in the slopes of these regressions between lotic and lentic assemblages. Slopes that are significant from zero ($p < 0.05$) are shown in bold. The predictors are: annual mean temperature (AMT), and annual precipitation (AP). The P - component represents the phylogenetically predicted part of the trait and S - component represents the respective deviation of the average trait from the P - component.

Model	Trait	Component	Predictor	Slope ± SE for lentic	Slope ± SE for lotic	R^2
Ordinary least-squares regression	Colour lightness	Average	AMT	**$3.0 \times 10^{0} \pm 2.8 \times 10^{-1}$**	**$2.7 \times 10^{0} \pm 4.4 \times 10^{-1}$**	0.29
			AP	$1.4 \times 10^{-1} \pm 2.9 \times 10^{-1}$	**$8.6 \times 10^{-1} \pm 4.2 \times 10^{-1}$**	
		S - component	AMT	**$1.2 \times 10^{0} \pm 1.2 \times 10^{-1}$**	**$6.6 \times 10^{-1} \pm 1.9 \times 10^{-1}$**	0.21
			AP	$3.2 \times 10^{-2} \pm 1.3 \times 10^{-1}$	$2.6 \times 10^{-1} \pm 1.8 \times 10^{-1}$	
		P - component	AMT	**$1.6 \times 10^{0} \pm 1.7 \times 10^{-1}$**	**$1.7 \times 10^{0} \pm 2.7 \times 10^{-1}$**	0.22
			AP	$-9.7 \times 10^{-2} \pm 1.7 \times 10^{-1}$	$-1.5 \times 10^{-1} \pm 2.5 \times 10^{-1}$	
	Body volume	Average	AMT	**$-2.5 \times 10^{-2} \pm 8.3 \times 10^{-3}$**	$-1.2 \times 10^{-2} \pm 1.3 \times 10^{-2}$	0.03
			AP	$6.3 \times 10^{-3} \pm 8.5 \times 10^{-3}$	**$3.6 \times 10^{-2} \pm 1.2 \times 10^{-2}$**	
		S - component	AMT	$-9.9 \times 10^{-4} \pm 6.4 \times 10^{-5}$	$-1.7 \times 10^{-4} \pm 1.0 \times 10^{-4}$	0.03
			AP	**$1.3 \times 10^{-4} \pm 6.5 \times 10^{-5}$**	$-9.3 \times 10^{-5} \pm 9.5 \times 10^{-5}$	
		P - component	AMT	**$-2.3 \times 10^{-2} \pm 8.3 \times 10^{-3}$**	$-1.1 \times 10^{-2} \pm 1.3 \times 10^{-2}$	0.04
			AP	$6.7 \times 10^{-3} \pm 8.5 \times 10^{-3}$	**$3.9 \times 10^{-2} \pm 1.3 \times 10^{-2}$**	
Spatial autoregressive error models	Colour lightness	Average	AMT	**$2.9 \times 10^{0} \pm 3.1 \times 10^{-1}$**	**$2.6 \times 10^{0} \pm 4.6 \times 10^{-1}$**	0.31
			AP	$3.0 \times 10^{-1} \pm 3.1 \times 10^{-1}$	$7.4 \times 10^{-1} \pm 4.3 \times 10^{-1}$	
		S - component	AMT	**$1.2 \times 10^{0} \pm 1.3 \times 10^{-1}$**	**$6.2 \times 10^{-1} \pm 2.0 \times 10^{-1}$**	0.22
			AP	$7.8 \times 10^{-2} \pm 1.3 \times 10^{-1}$	$2.3 \times 10^{-1} \pm 1.9 \times 10^{-1}$	
		P - component	AMT	**$1.6 \times 10^{0} \pm 1.8 \times 10^{-1}$**	**$1.7 \times 10^{0} \pm 2.7 \times 10^{-1}$**	0.24
			AP	$4.1 \times 10^{-2} \pm 1.9 \times 10^{-1}$	$-1.5 \times 10^{-1} \pm 2.6 \times 10^{-1}$	
	Body volume	Average	AMT	**$-2.2 \times 10^{-2} \pm 8.8 \times 10^{-3}$**	$-1.4 \times 10^{-2} \pm 1.3 \times 10^{-2}$	0.05
			AP	$8.1 \times 10^{-3} \pm 9.1 \times 10^{-3}$	**$3.3 \times 10^{-2} \pm 1.3 \times 10^{-2}$**	
		S - component	AMT	$-7.8 \times 10^{-5} \pm 6.8 \times 10^{-5}$	$-1.4 \times 10^{-4} \pm 1.0 \times 10^{-4}$	0.04
			AP	**$1.8 \times 10^{-4} \pm 7.0 \times 10^{-5}$**	$-9.1 \times 10^{-5} \pm 9.7 \times 10^{-5}$	
		P - component	AMT	**$-2.2 \times 10^{-2} \pm 8.8 \times 10^{-3}$**	$-1.4 \times 10^{-2} \pm 1.3 \times 10^{-2}$	0.05
			AP	$8.4 \times 10^{-3} \pm 9.2 \times 10^{-3}$	**$3.6 \times 10^{-2} \pm 1.3 \times 10^{-2}$**	

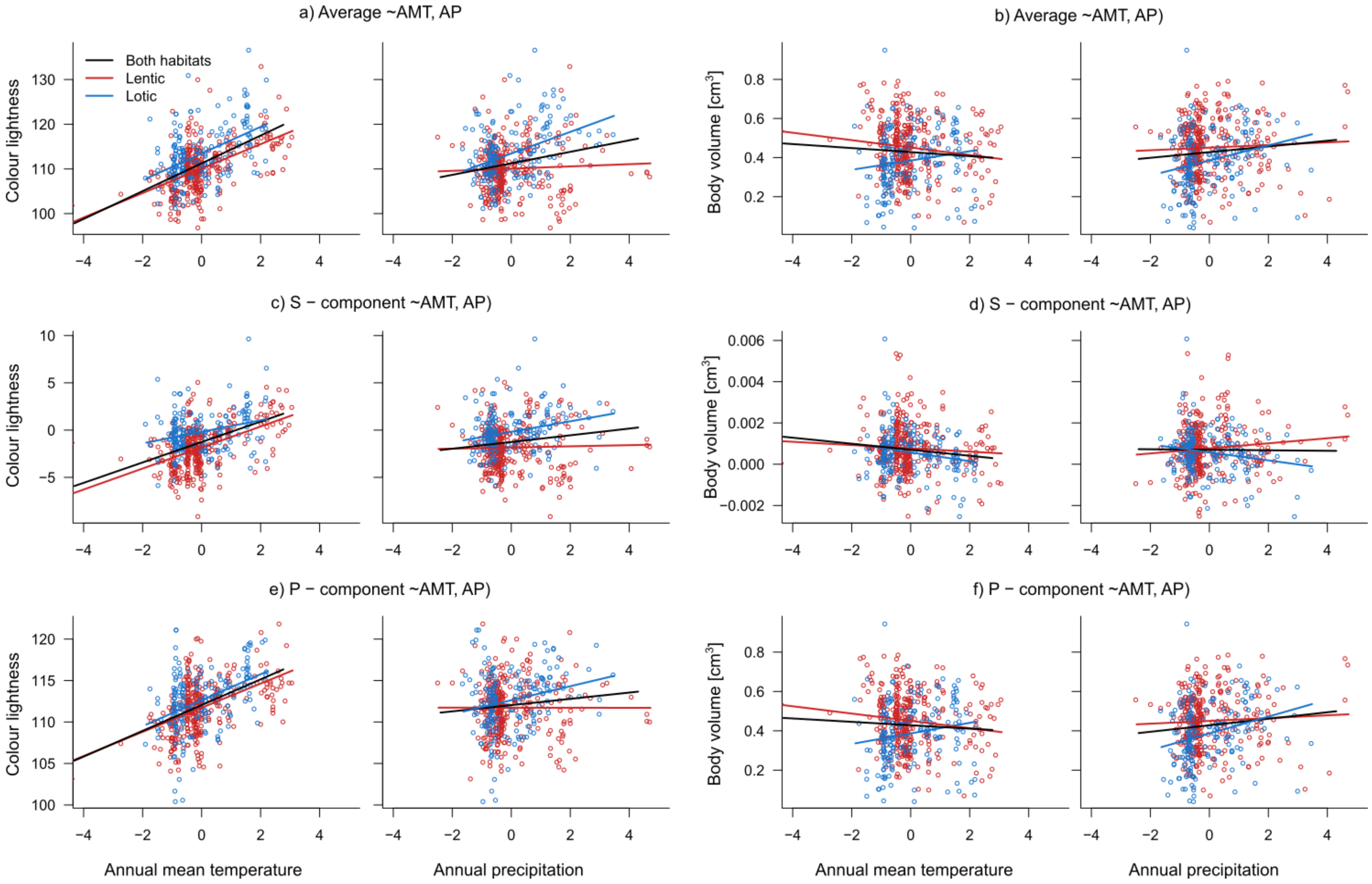

FIGURE 2.2 Scatterplots of the average (a, b), species-specific (c, d) and phylogenetic (e, f) components of the average colour lightness and body volume of (all habitats = 518, lentic = 337, lotic = 181) assemblages of European Odonates and z-standardised annual mean temperature, and annual precipitation. The colour of the dots indicates the habitat type of the assemblages. Lines indicate regression lines of ordinary least squares models. The colour lightness ranges from 0 (absolute black) to 255 (pure white). The P - component represents the phylogenetically predicted part of the trait and S - component represents the respective deviation of the average trait from the P - component.

2.5 DISCUSSION

Our results demonstrate that the spatial variation in colour lightness and body size (i.e., volume) of assemblages of Odonates across Europe is mainly driven by temperature. In line with the predictions of the thermal melanism hypothesis and Bergman's rule *sensu lato*, our results showed that the analysed assemblages in warmer regions were consistently composed of, on average, lighter coloured and smaller species of dragon- and damselflies compared to assemblages in cooler regions. Our continent-wide yet spatially explicit assessment of these relationships reconciles previous macroecological (Pinkert et al., 2017; Zeuss et al., 2014, 2017) and experimental (e.g. May, 1991; Samejima & Tsubaki, 2010; reviewed in Clusella-Trullas et al., 2007) evidence indicating the general importance of mechanistic links of colour lightness and body size with the physiology and distribution of ectotherm species. In addition to the overall importance of colour- and size-based thermoregulation, our comparison of the trait-environment relationships of lentic and lotic assemblages of Odonates revealed that the strength and relative importance of the climatic drivers of colour lightness and body size vary considerably between species with high and low dispersal/recolonisation ability.

Our study clearly showed that traits involved in thermoregulation influence the composition of dragonfly and damselfly assemblages across Europe. According to the thermal melanism hypothesis, darker ectotherms are at an advantage in cool regions because of colour-based heat gain, and lighter ectotherms in warm regions because they reflect more solar radiation. In support of this hypothesis, we found that the colour lightness of Odonata assemblages increased with increasing temperature. The results of our analyses based on survey data together with the similar geographical patterns in colour lightness reported for assemblages of other ectothermic organisms at large geographical scales (Clusella-Trullas, Terblanche, Blackburn, & Chown, 2008; Heidrich et al., 2018; Schweiger & Beierkuhnlein, 2015; Stelbrink et al., 2019; Xing et al., 2018; Zeuss et al., 2014), confirm that thermal melanism is a mechanism of major importance in ectothermic organisms across regions and scales.

Furthermore, consistent with the predictions of Bergmann's rule *sensu lato*, we found that the average body size of assemblages of Odonates decreased with increasing temperature. Even though a recent macroecological study by Zeuss et al. (2017) found support for Bergmann's rule in European Odonates, its support in insects is generally equivocal (Shelomi, 2012), especially in studies conducted at small spatial and taxonomic scales. These contradictions in the results obtained at different scales have recently motivated debate about the reliability of large-scale assemblage-level studies, as it has been demonstrated that the type of distribution information on which most macroecological studies are based can purely by chance result in geographical patterns of species' traits (Hawkins et al., 2017). Despite temperature explained a comparatively low variance in body size (c.f. Zeuss et al., 2017), our findings support Bergmann's rule *sensu lato* in European Odonates. Our support for both the thermal melanism hypothesis and Bergmann's rule using spatially explicit survey data for European Odonates show that the findings of studies based on expert range maps are robust to pseudo-replications of co-occurrences and the inherent geographical structures of species distributions (Hawkins et al., 2017).

Moreover, we also documented clear differences between species adapted to lentic and lotic habitats regarding the strength of the slopes of the considered trait-environment relationships and the relative importance of climatic drivers. Contrary to our third prediction, most of the relationships of average colour lightness and body size with temperature were equally strong between lentic and lotic assemblages. However, decomposing variations in colour lightness and body size showed that this is the result of similar responses of the phylogenetically predicted part of the traits of lentic and lotic species to climate, whereas relationships of the species-specific part of the traits were mostly stronger in lentic assemblages. Several studies have suggested that lentic species are stronger dispersers (e.g. Grewe et al., 2013; Hof et al., 2006; Marten et al., 2006) due to the negative relationship between habitat persistence and dispersal propensity (Southwood, 1962). Species adapted to lentic habitats are assumed to be closer to an equilibrium with ambient temperature (Dehling et al., 2010; Pinkert et al., 2018) and hence should dominate in recently recolonised regions (e.g., formerly glaciated northern parts of Europe; Pinkert et al., 2018). Accordingly, colour- and size-based thermoregulation together with high dispersal ability may have been hypothesised to cause contrasting biogeographical patterns between species adapted to lentic and lotic habitats over historical and evolutionary time scales (Hof et al., 2008; Pinkert et al., 2018). In fact, the distributional success and high diversity of lentic species in temperate regions seem to result not only from higher dispersal/recolonisation ability but also from an adaptive colour and body size evolution by lentic lineages. Our results suggest that adaptive colour and body-size are of similar importance for lentic and lotic species over evolutionary time scales, but that historical responses modified trait-environment relationships, with lentic species responding stronger to recent climatic changes than lotic species.

In light of previous zoogeographical and phylogeographical studies on dragon- and damselflies (Abellán et al., 2009; Kalkman et al., 2008; Pinkert et al., 2018; Sternberg, 1998), the documented differences in the trait-environment relationships of lentic and lotic species suggest that thermal melanism favours the colonisation of lineages of Odonates in temperate climates. It has long been hypothesised that Odonates are of tropical evolutionary origin and that only a few lineages acquired the ability to colonise and persist in temperate regions (e.g., Tillyard, 1917 p. 295). In a recent study, we found that the phylogenetic diversity of European Odonata assemblages decreased from the south-west to the north-east of the continent and that this pattern was mainly driven by the contemporary temperature (Pinkert et al., 2018). Latitudinal gradients of decreasing family or genus richness have been shown for

Odonates at the global scale (a simple proxy for the diversity of lineages; Kalkman et al., 2008). Furthermore, recent studies have documented a strong phylogenetic signal in the colour lightness of Odonates and butterfly assemblages as well as differences in the importance of thermal melanism between butterfly families and associated these differences with a lower importance colour-based thermoregulation in tropical lineages (Zeuss et al., 2014; Pinkert et al., 2017; Stelbrink et al., 2019). Therefore, our finding that phylogenetically predicted part of the variation in colour lightness and body size is strongly driven by temperature suggested that colour- and size based thermoregulation might have played a central role in the adaptation to colder climates, whereas most Odonata lineages retained their initial tropical niche (see also Pinkert & Zeuss, 2018). Besides the differences in the strengths of the relationships of colour lightness and body size with temperature, our results show that the relative importance of temperature versus precipitation in shaping the geographical patterns of these traits differs between lentic and lotic assemblages. Although both annual mean temperature and annual precipitation consistently drove overall geographical patterns in the colour lightness and body volume of assemblages of Odonates, lotic, but not lentic species seem to have an additional advantage of a higher size-based desiccation tolerance (Entling, Schmidt-Entling, Bacher, Brandl, & Nentwig, 2010), that also constrain their ability to thermoregulate via this trait. Specifically, we found that lotic assemblages in regions of lower precipitation were on average smaller than those in humid regions, which points to body size as an adaptation to water loss through the body surface (Kühsel et al., 2017).

Furthermore, we showed that species adapted to lotic habitats were significantly larger in regions that are both warm and wet. This finding supports the predictions of Gloger’s rule (Wilson et al., 2001), which have been generally strongly supported by several large-scale studies (Pinkert et al., 2017; Stelbrink et al., 2019; Zeuss et al., 2014). Although studies have shown that melanisation impacts desiccation resistance (Parkash, Rajpurohit &

Ramniwas, 2008; Parkash, Sharma & Kalra, 2009), we are cautious about interpreting a potential colour-based protection against water loss for two reasons; firstly, the environmental gradient of the study sites did not include extreme humid or dry regions and secondly, in our study annual precipitation was not an important driver of the variations in colour lightness European Odonata assemblages.

2.6 CONCLUSION

Our study highlights the importance of the mechanistic links of colour lightness and body size with the temperature regime which shapes the biogeographical patterns of dragon- and damselflies (Odonata). Colour- and size-based thermoregulation were by far the dominant mechanisms shaping the composition of assemblages of Odonates, although other functions of body size and colour lightness seemed to influence the geographical patterns of both traits to some extent. The consistency of our findings together with the results of a number of macroecological analyses recapitulate the general importance of thermal melanism and Bergmann's rule for ectothermic organisms. However, besides highlighting the crucial role of traits involved in thermoregulation in shaping the distribution of Odonate species, our results indicate that difference in species' dispersal propensities embedded in the spatio-temporal stability of their habitats contributes to explaining the scatter around the considered trait-environment relationships as well as to differences in the relative contributions of climatic predictors. Thus, thermal adaptations seem to be of similar evolutionary importance for lentic and lotic species but a greater dispersal ability of the former in combination with the climatic history of Europe seem to have allowed them better cope with historical climatic changes.

CHAPTER THREE

EXTRINSIC ENVIRONMENTAL FACTORS MODULATE THE RELATIONSHIP BETWEEN INTRINSIC FUNCTIONAL TRAITS AND THE EXTINCTION RISK OF EUROPEAN AND AFRICAN ODONATA

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Manuscript in preparation

3.1 ABSTRACT

Anthropogenic climate change has multiple impacts on biodiversity at different scales. The ability of insects to respond to these changes depends on the ecological preference and dispersal ability of the species. Whereas it is difficult to monitor species populations across entire ranges, the IUCN established criteria that allow taxon experts to broadly categorize the threat status of species. However, this assessment is dependent on the contemporary extent of occurrence and occupancy of species because the availability of time-series data is typically sparse and lacking for many species. To complement this assessment, we integrate trait-based models based on well-documented relationships of morphological and ecological traits with environmental factors to investigate how the species traits of African and European Odonates can improve predictions of their risk of extinction. Using body size, wing load and habitat preference as proxies for dispersal, and habitat stability, we incorporate current theoretical and empirical support for single effects of environmental variables on species traits into a structural ecological models. We tested whether species are generally larger in colder environments, whether species adapted to less stable habitats and with lower wing load have smaller ranges, and finally the extent to which these trait-environment relationships translate into a higher extinction risk of species. We found that the body size and wing load of odonates increased and decreased, respectively, with increasing latitude on both continents. Species adapted to lotic habitats and species with high wing loads have smaller range sizes. Increasing latitude and decreasing range size increase the risk of species extinction. However, the range size and maximum latitude occupied by species moderated the relationship between species body size, wing load and habitat preference and their extinction risk. Our findings highlight the potential of integrating trait information with estimates of species distribution and climatic requirements into trait-based models to not only help understand the physiological mechanisms underlying changes in species distributions, but also to improve predictions of species extinction risk.

3.2 INTRODUCTION

Human-induced climate change has a wide range of impacts on biodiversity at different levels of biological organization, from individuals to populations and ecosystem functions (Thomas et al., 2004; Fischlin et al., 2007; Urban, 2015). Some of the most frequently documented responses of species to climatic changes include shifts in species ranges to higher altitudes and latitudes (Hickling et al., 2005; Braune et al., 2008; Grewe et al., 2013; Termaat et al., 2019; Jourdan et al., 2019; Cerini et al., 2020), change in population trends (Powney et al., 2015; Bowler et al., 2021; Assandri, 2021) as well as local changes in the phenology of species (Hassall et al., 2007; Dingemanse & Kalkman, 2008). However, not all species can fully track climatic changes or compensate for them through plasticity, resulting in abundance declines, range contractions or eventually the extinction of local populations (Buckley & Kingsolver, 2012). In addition to climatic changes, land-use changes and habitat destruction increasingly threaten species with extinction (e.g. Newbold, 2018). The ability to cope with these changes ultimately depends on the ecological preference of the species, their dispersal ability and an understanding of which of these traits render a species vulnerable to extinction is thus critical for conservation management.

Whereas it is difficult to monitor species populations in detail and across entire ranges, the International Union on the Conservation of Nature (IUCN) established criteria that allow taxon experts to broadly categorize the threat status of species ranging from least concern, over near threatened, vulnerable, endangered and critically endangered, to extinct. This threat status is mainly determined by assessments of the contemporary extent of occurrence and occupancy of species because the availability of time-series data is typically sparse and lacking for rare and highly threatened species (Jeliazkov et al., 2022; Red List Guidelines from IUCN Standards and Petitions Subcommittee, 2022). Based on this measure, a species would be categorized as critically endangered if its range size is very small, population density (abundance) is low, and the habitat is highly threatened. IUCN threat status assessments thereby provide important baseline information for the prioritization of conservation efforts for species and taxa. Although the understanding of underlying causes of species extinction is fundamental for mitigating these negative developments, why some species are more threatened than others remains poorly understood.

Several well-documented relationships of morphological and ecological traits (hereafter intrinsic traits) with the habitat, range size and abundance (hereafter extrinsic traits) suggest that the extinction risk of species can have a common physiological/ecological basis. On the one hand, larger species are typically less abundant (White et al., 2007; Pinkert et al., 2020a) and species with a higher wing load, a proxy for the species dispersal ability, have smaller distribution ranges. Also, greater dispersal ability (often assessed using body size) is generally associated with stronger shifts in distributional ranges (MacLean & Beissinger, 2017). On the other hand, smaller surface area-to-volume ratios of larger bodies retain heat more efficiently than smaller bodies (Atkinson & Sibly, 1997; Zeuss et al., 2017; Acquah-Lamptey et al., 2020). Thus, larger species should have a thermoregulatory advantage in colder environments, for instance, higher elevations and latitudes compared to smaller species. Although only implicitly supported, the link between size-based thermoregulation and extinction risk may explain why in some taxa, and converse to the expectation that larger species are better able to cope with climatic changes through dispersal, larger species have a greater extinction risk (Chichorro et al., 2019). Specifically, warm-adapted species have demonstrated more positive population trends and more northward shifts in their ranges than cold-adapted species (Termaat et al., 2019; Bowler et al., 2020; Assandri, 2021, Engelhardt et al., 2022). Cold-adapted species, in turn, are not only more vulnerable because climatic changes are more severe in colder regions (IPCC, 2014), but also because these species in most cases are already at the geographical limits of their ranges

(Pinkert et al., 2018).

Another intrinsic factor, or rather a trait syndrome, influencing species range size (Hof et al., 2006), responses to climate change (Grewe et al., 2013; Pinkert et al., 2018), and potentially the extinction risk of species is their propensity to stable or less stable habitats. Similar to the distinction of r- and K-strategists, species associated with less stable habitats have evolved a range of adaptations such as pre-reproductive diapause, greater dispersal propensities, and greater stress tolerances that allow them to better cope with environmental changes (Southwood, 1977). Thus, in a broad spectrum of organisms, including plants (Morueta-Holme et al., 2013), vertebrates (Pinkert et al., 2020b) and invertebrates (Hof et al., 2006; Pinkert et al., 2018), the stability of a habitat or the climate in which a species lives is typically negatively related with the size of a species' range. Such species are open land species or freshwater organisms associated with standing waters that experience more seasonal, annual environmental fluctuation and that change in location over relatively short periods, compared to forests and running waters such as rivers (Seiboldt et al., 2019; Engelhardt et al., 2022). In freshwater organisms, where the habitat stability can be relatively easily assessed, species adapted to standing waters (hereafter lentic species) are better able to cope with environmental changes through shifts in ranges and redistributions (Hof et al., 2006; Grewe et al., 2013; Pinkert et al., 2018). On the contrary, species adapted to running waters (hereafter lotic species) tend to show population declines and range contractions. Thus, given the importance of habitat propensity for species' responses to climate change and range size, the incorporation of intrinsic traits into analyses of species threat status, should help to better understand why some species are threatened and mechanistic links may inform conservation about how mitigate species' threat.

Odonata is a relatively well studied freshwater taxon. Currently, Odonates are the most comprehensively assessed insect group (6,016 species; www.iucnredlist.org; accessed

January 6, 2022) with some 16% at risk of extinction. In contrast, only 1% of described insects have been assessed, with 26% categorized as data deficient (IUCN, 2022). In addition, analyses of species extinction risk as well as ecogeographical patterns in species' traits on invertebrates and even on odonates are almost exclusively studied in Europe and North America (Rocha-Ortega et al., 2020; Pinkert et al., 2017; Zeuss et al., 2017; Acquah-Lamptey et al., 2020). Given that endemic species are more vulnerable to extinction and a particular focus of conservation actions (Lamoreux et al., 2006; Lee and Jetz, 2008), this bias towards temperate region most likely has important implications for biodiversity research because tropical regions such as the Afrotropics harbour much greater numbers of endemic species (>80%; Clausnitzer et al., 2012) than Europe (11%; Kalkman et al., 2018).

Here, we investigate the mechanism underpinning links between species' functional traits and extinction risk, using data on over 489 dragonfly and damselfly (Odonata) species from Africa and Europe. Specifically, we test 1) whether species are generally larger in colder environments, 2) whether species with a lower wing load as well as those adapted to less stable habitats have smaller ranges. Finally, we assess the extent to which 3) these trait-environment relationships translate into a higher extinction risk of species. We do so by integrating current theoretical and empirical support for single effects among the considered variables into a generalized framework following the assumptions of trait-based theory (Figure 3.1).

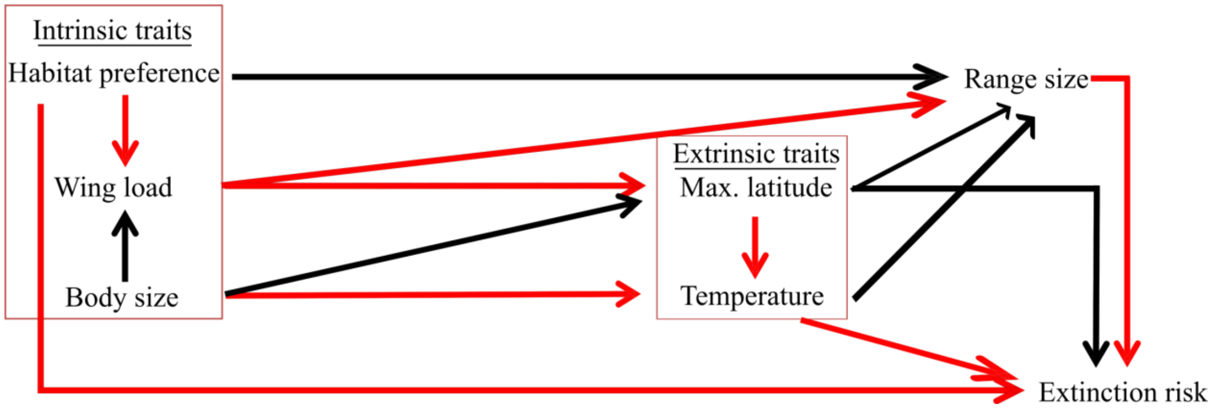

Figure 3.1 | Generalized framework of predicted effects of species morphological traits on their risk of extinction via species range size, maximum latitude, median annual mean temperature (extrinsic traits). Negative and positive relations are indicated by red and black respectively and all directions are based on existing theories in literature.

3.3 MATERIAL AND METHODS

An initial checklist of 838 Odonate species (dragonflies and damselflies) occurring across the African and European continents was compiled from the African Dragonflies and Damselflies Online database (ADDO, http://addo.adu.org.za), Dijkstra and Lewington (2006), and Dijkstra et al. (2020) respectively.

3.3.1 Intrinsic functional trait data

Body length and hind wing measurements were extracted from the African Dragonflies and Damselflies Online database (and supplementary literature therein). These measurements were complemented by the measurement of some specimens from collections at the Natural History Museum in Leiden (Naturalis, The Netherlands) and the Senckenberg Museum Frankfurt (SNMF, Germany). In addition, measurements of images of species were extracted from Dijkstra and Lewington (2006), Dijkstra et al. (2020), and Tarboton and Tarboton (2019). We extracted the habitat preference (lentic or lotic) of the odonates from the above mentioned literature sources. Subsequently, we converted these categories into an ordinal categorical value - only lotic, both, and only lentic, i.e., 0, 0.5, and 1, respectively. Previous studies show that dragonflies and damselflies adapted to lentic habitats have larger and more northern ranges (Hof et al., 2006), and demonstrate higher dispersal propensity than species adapted to lotic habitats (Hof et al., 2012; Grewe et al., 2013). We extracted the habitat preference (lentic or lotic) of the odonates from the above-mentioned literature sources. Subsequently we converted these categories to an ordinal categorical value - only lotic, both, and only lentic, i.e., 0, 0.5, and 1, respectively. We considered measurements for males only because of their availability but note that measurements of both sexes are highly positively correlated (Zeuss et al., 2017). Individual measurements of body and hind wing length were aggregated to average trait values. Subsequently, we calculated species' wing loads as body-to-hind wing length ratios. Wing load is a common proxy for the dispersal ability of winged species, with lower values translating to improved flight ability due to lower energy expenditure during flight (Casey, 2018).

3.3.2 Extrinsic variables

Range size is the most common and straightforward metric to evaluate regional extinction risk, with a smaller range size indicating a greater the susceptibility to ecological disturbance and environmental change and thus higher the risk of extinction (IUCN, 2018). As a proxy for the range size of species, we downloaded expert range maps provided by the IUCN and resampled them to a 100 km × 100 km equal-area grid (Military Grid Refence System). In addition, we aggregated annual mean temperature data from www.chelsa-climate.org (Karger et al., 2017, 2018) and elevation data from EarthEnv.org (Robinson et al., 2014) for each grid cell. According to the predictions of temperature-size rule and findings from previous studies (Termaat et al., 2019; Zeuss et al., 2014; Acquah-Lamptey et al., 2020), we considered temperature, elevation and latitudinal range as a predictor of geographical patterns in body size of odonates. Specifically, we calculated the median annual mean temperature across species' ranges as a proxy for environmental temperature. In addition, we used the resampled distributional data to calculate the minimum and maximum latitude a species' ranges, which are often also used in studies of range shift (Hickling et al., 2005; Simaika & Samways, 2015; Termaat et al., 2019). Estimates of species elevation ranges were compiled from literature and, complemented by elevation data extracted through occurrence records (from Sandall et al., 2022). Because data on minimum elevations from literature were frequently unavailable, we only used the maximum elevation to characterize species' altitudinal ranges (Harabiš & Dolný, 2010; Simaika & Samways, 2015).

3.3.3 Species threat status

The International Union for Conservation of Nature (IUCN) has a well-known objective qualitative assessment system for classifying the status of organisms based on their risk of extinction. This assessment is usually based on current information by specialists who assess the extinction risk assessment of each taxon based on a set of criteria linked to population trends, population size and structure, and geographic range. From the database, we compiled the threat status of African and European odonates. Species were classified as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Data Deficient (DD), or Not Evaluated (NE). We excluded species listed as DD and NE in the Red list classification or with missing trait information from the analyses and converted the remaining categories to ordered numeric classes (from Least concern = 1 to Critically Endangered = 5). Given that endemic species have increased vulnerability due to their smaller populations and limited ranges, we present the spatial variation of the threat status and distribution of endemic European and African Odonata (Figure 3.2). Despite being the most assessed insect group, some nearly 30% of these species have been categorized as data deficient (IUCN, 2022). Based on the importance of range size in species extinction risk assessment, in a supplementary analysis, we show a pair-wise comparison of the range size of the various species threat categories (Figure S3.2).

3.3.4 Statistical analyses

To avoid overfitting of models which may render their interpretations impossible (Phillips et al., 2006), we used the *rcorr* function of the R-package *Hmisc* to test multicollinearity of our independent variables. The variables body length (log) and wing length (log) were highly correlated (Pearson correlation coefficient = 0.86) and annual mean temperature and maximum latitude were highly negatively correlated (Pearson correlation coefficient = 0.78; Figure S3.1). However, we checked mulitcollinearity among predictors, using the *vif* function of the R package *car* (Table S1; Fox et al., 2016). The variables annual mean temperature and maximum latitude were maintained due to the low variance inflation factors and their independent importance of in the path analysis (Table S3.2)

Tests for species trait-extinction risk relationships were performed using single and multiple generalized linear regression and linear mixed effect models allowing for nested random effects such that within-group errors are allowed to have unequal variances (Laird & Ware, 1982). The species extinction risk was the dependent variable and the independent intrinsic variables were the average body size, the average hind wing length, the average wing load, and the proportion of lentic to lotic species (habitat preference) of European and African odonates. Similarly, we considered the geographical location of the species (continent; higher values refer to Europe), maximum elevation, minimum and maximum latitudinal range, the median annual mean temperature of the species distribution range, and finally the range size of species as the independent extrinsic variables. The distributions of all variables were checked and transformed, if necessary. To normalise the data, body size, wing load, hind wing length, maximum elevation, median annual mean temperature, and range size were log-transformed. In the analyses we used absolute values of minimum and maximum latitude assuming that latitudinal gradients are mirrored in the northern and southern hemisphere.

Subsequently, we tested whether the extrinsic traits; range size, latitude, and temperature mediate the effects of intrinsic traits; body size, habitat preference, and wing load on species risk of extinction using confirmatory path analyses (Shipley, 2004) as implemented in the R package *piecewiseSEM* (Lefcheck, 2016). This approach allows us to fit a set of linear models in a single causal framework to test multiple hypotheses about relationships of interacting variables and for evaluating the direct and indirect effects of predictor variables on the responses (Figure 1). Specifically, we fitted multiple model sets as the basis for confirmatory path analyses showing both direct and indirect paths between intrinsic and extrinsic traits and species extinction risk. In the piecewise structural ecological models, we tested how species dispersal propensity (using wing load as a surrogate) is influenced by habitat preference and its body size. Secondly, we tested the relationship between annual mean temperature and body size. We also looked at the relationship between body size, wing load, and maximum latitude. We then tested how habitat preference, wing load, annual mean temperature, and maximum latitude influence species range size and lastly how habitat preference, range size, annual mean temperature, and maximum latitude influence extinction risk. Although most of the predicted relationships were significant for the model including dispersal propensity and species thermal environment, Fisher's C statistics from the test of directed separations, indicated that some relevant paths were missing. Following Shipley (2004), we therefore added the predictor variables (Table S3.3). All tests were done with and without accounting for phylogenetic relationship between the species (Table S3). Since body size and habitat preference of European odonates carry a phylogenetic signal (e.g., Zeuss et al. 2014; Pinkert et al., 2017), we accounted for the phylogenetic relationship between species in all analyses using the most recent resolution in the global phylogeny for Odonata (Bybee et al., 2021; Letch et al., 2016). To account for phylogenetic structure in the data, genus, family, and species-level random effects were incorporated in the models. All statistical analyses were conducted in R (version 4.1.0, R Core Team, 2021).

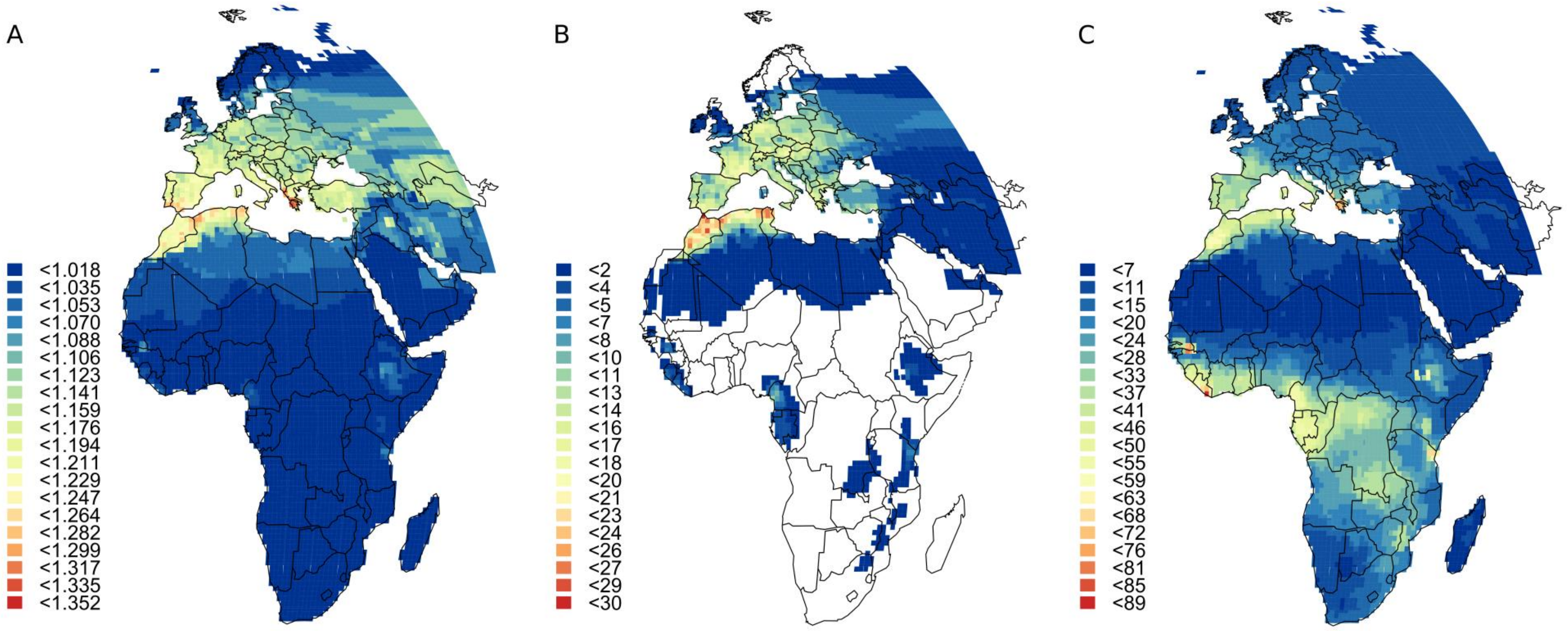

Figure 2 | Spatial variation of the threat status of European and African Odonata (A). Assemblages represent the threat status distribution of 433 species. Colour scale intervals follow an equal frequency classification, with blue indicating less threatened species and red indicating more endangered species. B - Spatial variation of Odonata species with threat status (near threatened, vulnerable, endangered, and critically endangered). Colour scale intervals follow an equal frequency classification with threat status increasing from blue to red. C - Spatial variation of endemic European and African Odonata. Colour scale intervals follow an equal frequency classification with blue indicating less endemic species and red indicating more endemic species. The dataset comprises 6,573 grid cells of 100 km × 100 km size (Mollweide projection).

3.4 RESULTS

3.4.1 Single and multiple regressions

Among the intrinsic traits expected to influence species risk of extinction, only habitat preference had a direct effect. Thus, lotic species were more threatened than lentic species (Table 3.1). Among the extrinsic environmental traits, the species range size and the maximum elevation occupied by odonates negatively affected species' extinction risk. A higher proportion of European odonates were more threatened than the African species (Table 3.1). Consistently, habitat preference only significantly influenced the threat status of European and African odonates from a multiple regression involving the intrinsic traits. However, a multiple regression involving extrinsic variables only showed that range size, continent, maximum latitude, and annual mean temperature of the species range significantly affected the risk of extinction of European and African odonates (Table 3.1). But a multiple regression (including both intrinsic and extrinsic) produced significant relationships between range size, continent, annual mean temperature, and odonates extinction risk. Thus, European species were more threatened than African species, species with smaller range sizes had a higher risk of extinction (Figure 3.3), and species with higher environmental temperature had higher extinction risks (Table 3.1, Figure 3.3). The effect of the intrinsic and extrinsic traits on the extinction risk of European and African odonates explained up to 36 % (single regressions), between 3 % – 39 % (intrinsic and extrinsic traits respectively), and 39% (all traits) of the variance in multiple regressions (Table 3.1).

3.4.2 Structural equation model

3.4.2.1 Trait-environment relationship

From the structural ecological models, the body size of European and African odonates positively affected the maximum latitude of a species' range but no direct significant relationship is found between body size and annual mean temperature. Species with larger body sizes had higher wing loads. Also, wing load negatively affected the maximum latitude of a species' range and negatively affected range size. Habitat preference did not affect species' wing load in Odonates, species adapted to lentic habitats (high values) had larger range sizes than lotic species (lower values; Figure 3.3).

3.4.2.2 Environment-extinction risk relationship

The effect of the intrinsic traits of species risk of extinction was mediated by the effect of the extrinsic traits. Whiles range size increases with increasing annual mean temperatures and it also increases when species occupy higher maximum latitudes. However, there is a negative relationship between maximum latitude and annual mean temperature (Table 3.2, Figure 3.3). Species with larger range sizes have a lower risk of extinction.

3.4.2.3 Mediation of morphological/dispersal traits on extinction risk

Lentic species have larger range sizes hence at a lower risk of extinction. Similarly, wing load positively affected the maximum latitude and the size of species' ranges. Thus, species with higher maximum latitudinal limits and lower range sizes had a higher risk of extinction. Species' body size positively affected the maximum latitude of a species' range which resulted in a higher risk of extinction (Table 3.2, Figure 3.3). These relationships are consistent when the structural models are fitted differently accounting for phylogenetic relationship between the species (Tables S3.3). However, without accounting for the phylogenetic relationship between species, no significant relationship between wing load and body size is observed. Also, species adapted to lotic habitats have higher wing loads while larger species have higher maximum latitude (Table S3.3).

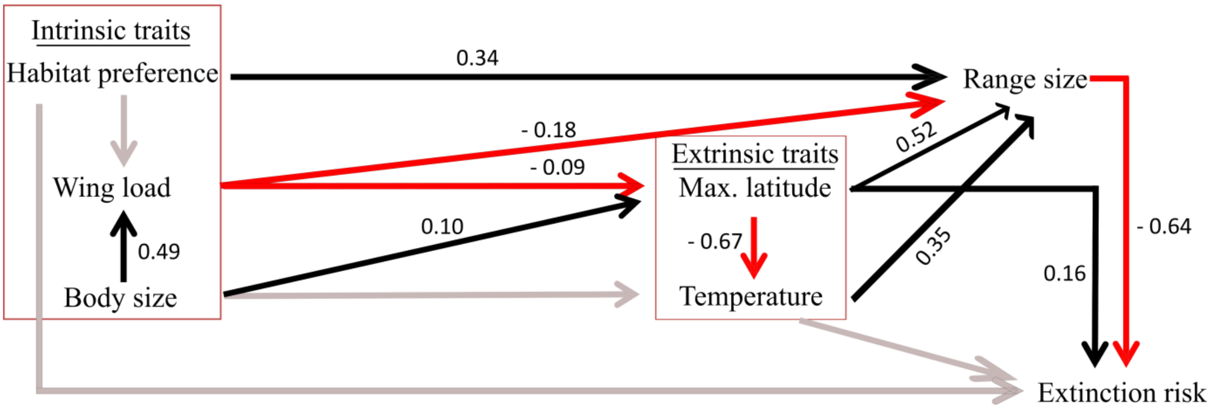

Figure 3.3 | Extrinsic traits mediate the effect of intrinsic traits on the risk of extinction on European and African dragonflies and damselflies. Results from piecewise structural equation models that test for direct effect of intrinsic traits on Odonate risk of extinction and indirect effects via extrinsic traits as proxies. All component models of the two piecewise structural equations controlled for species' phylogenetic relatedness with a random effect of genus nested in family and suborder. Values indicate scaled regression coefficients of significant paths ($P < 0.05$). Non-significant paths are indicated by grey arrows. Fisher's C = 16.883, df = 12, $P = 0.154$, AIC = 74.883, BIC = 196.462.

Table 3.1 | Individual slopes (±SE) of predictors from single and multiple regression models as well as the explained variance from single (r^2) and multiple (R^2) regression models testing for the relationship between the conservation status of European and African Odonates and intrinsic traits and extrinsic environmental variables. Significant slopes ($p < 0.05$) are bold.

			Single regressions			**Multiple regression**					
		Traits	Slope ± SE	*t*-value	r^2	Slope ± SE	*t*-value	R^2	Slope ± SE	*t*-value	R^2
Overall	Intrinsic	Hind wing	$-2.9 \times 10^{-3} \pm 1.6 \times 10^{-2}$	−0.02	<0.001						
		Wing load	$2.5 \times 10^{-1} \pm 2.5 \times 10^{-1}$	1.02	0.003	$1.8 \times 10^{-1} \pm 2.5 \times 10^{-1}$	0.71		$-2.9 \cdot\times 10^{-1} \pm 1.8 \times 10^{-1}$	−1.63	
		Habitat Preference	**$-3.1 \cdot\times 10^{-1} \pm 9.3 \times 10^{-2}$**	**−3.30**	0.027	**$-3.0 \times 10^{-1} \pm 9.4 \times 10^{-2}$**	**−3.15**		$1.7 \times 10^{-2} \pm 7.2 \times 10^{-2}$	0.23	
		Body size	$8.9 \times 10^{-2} \pm 1.5 \times 10^{-1}$	0.59	0.001	$-4.2 \times 10^{-2} \pm 1.5 \times 10^{-1}$	−0.03	0.03	$-5.2 \times 10^{-2} \pm 9.8 \times 10^{-2}$	−0.53	
	Extrinsic	Range size	**$-2.7 \cdot 10^{-1} \pm 1.6 \times 10^{-2}$**	**−17.2**	0.355	**$-2.9 \times 10^{-1} \pm 1.8 \times 10^{-2}$**	**−16.44**		**$-2.6 \times\cdot 10^{-1} \pm 2.0 \times 10^{-2}$**	**−13.02**	
		Continent	**$2.1 \times 10^{-1} \pm 8.5 \times 10^{-2}$**	**2.52**	0.012	**$3.2 \times 10^{-1} \pm 7.3 \times 10^{-2}$**	**4.38**		**$3.5 \times 10^{-1} \pm 6.8 \times 10^{-2}$**	**5.23**	
		Maximum elevation	**$-2.4 \times 10^{-1} \pm 4.2 \times 10^{-2}$**	**−5.71**	0.051	$3.4 \times 10^{-2} \pm 4.0 \times 10^{-2}$	0.85		$-4.0 \times 10^{-2} \pm 4.2 \times 10^{-2}$	−0.94	
		Maximum latitude	$-3.9 \times 10^{-3} \pm 2.1 \times 10^{-3}$	−1.84	0.009	**$5.1 \times 10^{-3} \pm 2.4 \times 10^{-3}$**	**2.14**		$3.3 \times 10^{-3} \pm 2.4 \times 10^{-3}$	1.36	
		Minimum latitude	$1.3 \times 10^{-3} \pm 2.8 \times 10^{-3}$	0.48	<0.001	$4.7 \times 10^{-3} \pm 2.4 \times 10^{-3}$	1.95		$3.6 \times 10^{-3} \pm 2.3 \times 10^{-3}$	1.55	
		Annual mean temperature	$-6.1 \times 10^{-3} \pm 9.6 \times 10^{-2}$	−0.06	<0.001	**$2.8 \times 10^{-1} \pm 1.1 \times 10^{-1}$**	**2.62**	0.39	$2.4 \times 10^{-1} \pm 1.0 \times 10^{-1}$	2.26	0.39

Table 3.2 | Summary of the complete Piecewise structural ecological based on a generalized framework of predicted effects of species morphological and dispersal traits on their risk of extinction via species range size, maximum latitude, and median annual mean temperature. In all models we account for the phylogenetic relationship between species. Significant standardised estimates (p< 0.05) are bold.

		Wing load	Body size	Habitat preference	AMT	Maximum latitude	Range size	Extinction risk
Complete GLM model (accounting for phylogenetic relationships). Fisher's statistics: C = 16.883, df = 12, p-value = 0.154, AIC = 74.883, BIC = 196.462	Wing load		**0.4856**	–0.0005		**–0.0865**	**–0.1763**	
	Body size	**0.4856**			**–0.0509**	**0.1041**		
	Habitat preference	–0.0005					**0.3400**	0.0245
	AMT		**–0.0509**			**–0.6648**	**0.3517**	**0.1007**
	Maximum latitude	**–0.0865**	**0.1041**		**–0.6648**		**0.5202**	**0.1591**
	Range size	**–0.1763**		**0.3400**	**0.3517**	**0.5202**		**–0.6429**
	Extinction risk			0.0245	**0.1007**	**0.1591**	**–0.6429**	

AMT = Annual mean temperature (median), AIC = Akaike information criterion, BIC = Bayesian information criterion, df = Degrees of freedom.

3.5 DISCUSSION

In our study we integrated intrinsic and extrinsic traits into a generalized trait-based modelling framework to improve our understanding of the mechanisms underlying variation in species’ extinction risk. Extrinsic traits are frequently used in studies of species’ extinction risk because they can be readily calculated from a species range. However, we argue that species ranges are generally only available for a small proportion of taxa and studies on extrinsic drivers of extinction risk lack explanations of why some species are more threatened than others – an understanding that is essential to mitigate extinction risk through targeted management. Our results generally support strong direct effects of the range size and the maximum latitude of species’ ranges with the extinction risk documented in previous studies. However, by also integrating putative intrinsic drivers of species’ extinction risk our framework also highlights that the ultimate cause of these effects of extrinsic traits on species’ threat status are differences in species’ dispersal ability, body size and habitat preference. Thereby, we exemplify the potential of using trait information that is typically available from field guides and species descriptions to improve forecasts of species’ threat as well as for guiding conservation action through general ecological mechanisms and flagging species as potentially vulnerable based on intrinsic trait alone.

Our results provide the first evidence for several trait-environment relationships that thus far only have been investigated for temperate insect taxa, including the temperature-size rule as well as effects of dispersal ability and habitat preference on the size and geographical position of a species range. In line with the predictions of the habitat-stability hypothesis and previous findings on freshwater organisms in temperate regions (Hof et al., 2006; Grewe et al., 2013), we show that species adapted to standing (lentic) waters generally have a larger range size and consequently a lower risk of extinction. In turn, species adapted to running waters are more threatened with extinction. Besides the ability of pre-reproductive diapause and drought tolerance (Corbet, 1999), one of the main factors driving this pattern is thought to be dispersal (Hof et al., 2006; Hof et al., 2012). Through the integration of estimates of species wing loads (body size to wing size ratios) as a proxy a species dispersal ability, we demonstrate that indeed species with lower wing load generally have larger and more northern ranges. In addition, the wing load of lentic species did not differ from that of lotic species, which underlines that the ecological classification of species' habitat preference also includes unique information on their propensity for dispersal, tolerances, and life-history strategies.

Body size is frequently used in analyses of species' extinction risk (Chichorro et al., 2019) and range shifts (MacLean & Beisinger, 2017). In this context a larger body size is generally interpreted as surrogate for a greater dispersal ability of species and hence larger species should have a lower extinction risk and show stronger range shifts. However, the effect of body size in such analyses is ambiguous and typically not significant at all, particularly in flying taxa (MacLean & Beisinger, 2017; Chichorro et al., 2019). Here we argue that part of this heterogeneity is explained by the confounding effects of disproportionately large or small wings and the thermoregulatory importance of body size (Pinkert et al., 2020a). The higher cost for dispersal or mobility of species with a larger body relative to their wing size are well-documented by physiological studies, but because body size and wing load are typically moderately correlated, body size is still frequently considered a proxy for the dispersal ability. Here we show that this assumption may lead to misinterpretations of the role of dispersal versus thermoregulation. On one hand, body size had only minor effects on range size, whereas it was the most important predictor of species thermal requirements. On the other hand, species with a greater dispersal ability (i.e. smaller wing loads) occur at higher latitudes while smaller species occur at lower latitudes. Though the herein documented geographical patterns of body size and wing load across an entire latitudinal gradient are the first for any insect taxon, they reconcile several smaller-scaled studies. Our result that species with a lower wing load have larger ranges is consistent with previous findings on plecopterans in New Zealand (McCulloch et al., 2017). Furthermore, the negative relationship between body size and temperature, resembles patterns documented for butterflies and beetle assemblages across Europe (Zeuss et al., 2014; Schweiger & Beierkuhnlein, 2015), as well as body size clines along elevational gradients documented for moths, butterflies, and ants (Bishop et al., 2015; Horne et al., 2015; Brehm et al., 2019; Heidrich et al., 2021). Thus, in line with our expectation that larger species have a thermoregulatory advantage in colder climates, body size generally increased with increasing latitude and decreasing temperature. In the context of these studies, our results highlight the importance of body size for thermoregulation, and they discourage its interpretation as a proxy of dispersal ability. We stress the need to disentangle the multitude of mechanism underlying body size variation through integrating better proxies for functional traits such as dispersal as well as relevant extrinsic proxies to understand species' responses to environmental changes. Similarly, analyses of population trends and range shifts that frequently use estimates of the thermal preference of species by broadly classifying warm-adapted and cold-adapted species (Bowler et al., 2021; Engelhardt et al., 2022), could potentially be improved by simultaneous analyses of body size and wing load.

3.5.1 Mediation of morphological/dispersal traits on extinction risk

Using a generalized ecophysiological framework, we show how ecological mechanism such as relationships of habitat stability and dispersal with range size and maximum latitude, as well as of body size with maximum latitude and temperature preference translate into extinction risk (Table 3.1). The considered intrinsic traits strongly affected species' extinction risk but all these effects were mediated by extrinsic traits (Figure 3.3, Table 3.2). For instance, species with lower wing loads generally had larger ranges and therefore a reduced extinction risk, whereas species with a lower wing load were also found in higher latitudes where species have an increased extinction risk. Similar contrasting effects were found for body size. Although the net effect of wing load was positive (a higher wing load increases extinction risk; [–0.18 * –0.64 = 0.12] + [–0.09 * 0.16 = –0.01] + [–0.09 * 0.52 * –0.64 = 0.03] = 0.14]) and that of body size was positive (i.e. larger species have a lower extinction risk; [0.10 * 0.16 = –0.02] + [0.1 x 0.52 * –0.64 = –0.03] + [0.1 * –0.67 * 0.35 * –0.64 = 0.02] + [0.1 * 0.14 = 0.01] = 0.02]), our results highlight that multiple trait-environment relationships determine a species' threat status in concert. Together with multiple regressions that tested for direct relationships of intrinsic traits and the extinction risk, we demonstrate that important effects of body size and wing load are obscured when ignoring the environmental component of species' responses (Table 3.1). Thus, in line with the results reviewed in Chichorro et al. (2020), these simplified models did not support relationships of body size and wing load on species threat status. This was markedly different for the preference of species to stable and less stable habitats. Thus, habitat preference was only related to range size and both in the path analyses and in the multiple regression where species adapted to lentic (less stable) habitats had a lower extinction risk than those adapted to lotic (stable) habitats (Table 3.1). The indirect, but strong and consistently positive effect of habitat preference on range size and ultimately on extinction risk may therefore explain previous support of a lower threat of lentic species compared to lotic species (Korkeamäki & Suhonen, 2002; Rocha-Ortega et al., 2019). Given that lotic odonates have weaker dispersal propensities that hamper the colonization of suitable regions and impede range shifts (Grewe et al., 2013), Odonata conservation, should target more effort at species adapted to lotic habitats.

3.5.2 Conservation implications

The main implications of our results for applied conservation are that well-known ecological mechanisms translate into species' extinction risk. Odonata are an ideal system for studies of species extinction risk because of their congruence with both freshwater and terrestrial taxa and because they represent the only insect order with an almost complete assessment of the extinction risk by the IUCN. The evaluation of species' threat status are extremely sparse for the majority of taxa due to both the lack of experts and the time-consuming process of generating species range maps that form the basis of initial threat assessment. But even if range maps exist, a large number of species remains classified as data deficient regarding the threat status. Therefore, on the one hand, the documented relationships of extrinsic factors can help to refine or predict the extinctions risk. On the other hand, we show that general ecological mechanisms largely determine the range size of species, which is in turn strongly related to extinction risk. Thus, integrative modeling approaches that use readily available trait information combined with estimates of the distribution and climatic requirements extracted from occurrence points are of high potential to provide initial flags that may facilitate the risk assessments. Our results for the habitat preference of Odonata show that even broad classifications of ecological important preferences can significantly improve these predictions and similar studies on other freshwater organisms suggest that such measures alone can help prioritization of conservation action. Specifically, based on our results conservation action may focus on improving the water quality of rivers and streams. Additional intrinsic and extrinsic traits, but also information on the phylogenetic relationship of species can serve to refine this action. Thus, our results furthermore highlight that cold adapted (i.e. large and in high latitude) with a poor dispersal ability (i.e. high wing load and small range) and propensity (i.e. lotic and small range) are more threatened with extinction. Since most of the considered traits carry strong phylogenetic signals, climatic changes, and consequent responses, seem to threaten certain lineages such as members of the dragonfly genus *Syncordulia* which is endemic to Montane lotic habitats in South Africa (Tarboton and Tarboton, 2015; Clausnitzer, 2018). Based on our findings, we suggest that such species are limited both in their dispersal ability, dispersal propensity as well as geographical barriers (i.e. shifts impossible if species are already at the mountain tops). Targeted conservation may thus focus on improving habitat conditions, connect populations with habitat steppingstones, or even assist species’ migration.

3.6 CONCLUSION

Traits are important determinants of extinctions risk. Our models could explain 39 % of the variations in extinction risk mainly due to range size, but also other extrinsic traits. However, importantly intrinsic traits explain why species vary in range size. Our study therefore establishes links between ecology and conservation that are relevant for completing and predicting species threat status. Most extrinsic variables can be extracted from occurrence data and traits can help to predict range size and subsequently serve as a red flag for conservation assessment. Such integrative trait-based workflows are particularly relevant for closing an important knowledge gap for invertebrate species where only a small fraction (2%) of identified species has been assessed. Thereby, our study exemplifies the potential use of traits to improve the knowledge base necessary for targeted conservation using ecological theory and the treasure trove of biodiversity data.

CHAPTER FOUR

EFFECT OF A DRAGONFLY (*BRADINOPYGA STRACHANI* KIRBY, 1900) ON THE DENSITY OF MOSQUITO LARVAE IN A FIELD EXPERIMENT USING MESOCOSMS

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4.1 ABSTRACT

Laboratory experiments with food-deprived larvae of Odonates suggested that these predators may have the potential to control mosquito populations. However, it remains unclear whether larvae of Odonates co-occur with mosquito larvae in the field and whether larvae of Odonates reduce the density of mosquito larvae in the field. We exposed 35 water-filled concrete containers in the field in shady and sunny conditions. Some of these containers were partially covered (for simplicity called closed containers, allowing only mosquitoes to lay eggs), whereas others remained open. The density of mosquito larvae was higher in shaded containers and in closed containers. The multivoltine Odonate Bradinopyga strachani colonized open containers and the occurrence of these predators resulted in a clear reduction of the mosquito population. Our results indicate that increasing the colonization of water bodies by Bradinopyga strachani is a promising strategy for controlling populations of mosquitoes.

4.2 INTRODUCTION

Mosquitoes are vectors of severe diseases, such as malaria, yellow fever, chikungunya, dengue fever, lymphatic filariasis, Rift Valley fever, and Zika fever (World Health Organization, 2016a). The main vectors of these diseases are species of the nematoceran genera Aedes, Culex and Anopheles (World Health Organization, 2016a). Each year, over a million deaths occur and several hundred million people worldwide suffer from mosquito-borne diseases (World Health Organization, 2013, 2016b, c, d, 2017). In Africa, dengue fever is endemic in 34 countries, 35 countries have a high risk of yellow fever, lymphatic filariasis is endemic in 39 countries, and 188 million cases of malaria occur across the entire region (World Health Organization, 2013, 2016b, c, d, 2017). In Ghana, malaria alone is responsible for about 14 000 deaths of children per year (Ministry of Health & Ghana Health Service, 2013). Treatment of these mosquito borne diseases comes at a substantial cost (Kokwaro, 2009) and the vaccination against malaria has had little success (Gosling and Von Seidlein, 2016). Furthermore, the mosquito vectors are resistant to insecticides (Kelly-Hope et al., 2005; Mawejje et al., 2013; Kudom et al., 2015a, b), and the pesticides also affect non-target species (Ware, 1980). Hence, affordable and environmentally friendly methods of controlling larval (and adult) mosquitoes need to be developed.

One strategy that has shown some potential in reducing the density of mosquito larvae is the use of various lineages of predators such as crustaceans, fish, amphibians and also Odonates (dragonflies and damselflies; Table 1). The aquatic larvae of Odonates can co-occur with the larvae of mosquitoes. Several studies of Odonate predation on mosquito larvae have used food-deprived individuals of the predator (e.g. Venkatesh and Tyagi, 2013a, b; Saha et al., 2012; Kweka et al., 2011; Mandal et al., 2008). For instance, Kweka et al. (2011) collected Odonates from breeding grounds, starved them for 12 h before introducing them into experimental habitats. Saha et al. (2012) collected Odonates, starved them for 24 h in the laboratory before offering various instars of *Culex quinquefasciatus* to examine the functional response. Mandal et al. (2008) also collected and transported two dragonfly and three damselfly species from their natural breeding sites into the laboratory to test the efficiency of the larvae of these species in controlling *Culex quinquefasciatus*. However, interpretation of the results from these experimental studies suffers from various methodological limitations (reviewed in Kumar and Hwang, 2006). Despite clear indications that Odonates feed on mosquito larvae, the results of such studies overestimate predation rates as well as the potential to reduce densities of mosquito larvae under field conditions (Weterings et al., 2015).

Several factors could affect the success of the biological control of mosquitoes using Odonates, such as (1) the particular mosquito species and the density of mosquito larvae, (2) density, body size, and species identity of the Odonate (Cordoba-Aguilar and Lee, 1994; Fincke et al., 1997; Saha et al., 2012; Weterings et al., 2015), (3) habitat and water quality (Fincke et al., 1997; Kweka et al., 2012; Varshini and Kanagappan, 2014; Akram and Ali-Khan, 2016) and (4) overlap of mosquito and Odonate habitats (Chatterjee et al., 2007). Furthermore, mosquitoes breed in a wide range of habitats that are usually of low quality (Dejene et al., 2015; Kudom, 2015), e.g. rain pools, concrete tanks, and choked gutters. Therefore, species of Odonates that are able to naturally breed in such low-quality habitats are potential agents for the biological control of mosquito larvae. Although Odonates are known to be more effective than other predators in controlling their prey (Kumar and Hwang, 2006), it is thought that larvae of Odonates and mosquitoes do not coexist naturally at high densities and that Odonate larvae are not selective enough in their feeding behaviour to reduce the density of mosquito larvae (Sebastian et al., 1990). In a simple field experiment, we tested the hypothesis that Odonates colonize artificial habitats like water-storage containers used in African villages and are able to reduce the density of mosquito larvae which also colonize these containers.

4.3 MATERIALS AND METHODS

4.3.1 Study area

The study was conducted on the research farm of the University of Ghana, Legon campus (5°39'28.7" N 0°11'31.6" W), which lies within the main university campus, 13 km northeast of the capital Accra. The 29 ha farm is characterized by natural grass fields, irrigated vegetable fields and widely interspersed trees of mango and cashew. The experiment was conducted between June and August 2016, when coastal regions of Ghana experience peak rainfall (annual rainfall: 733–1118 mm).

4.3.2 Field experiment

We randomly placed 18 concrete containers (120 cm x 60 cm x 40 cm) in shaded areas and 17 containers in sunlit areas. The containers were filled with ground water (Supplement Figure S4.4). Ten containers (four in sunlight and six in shade) were each partially covered with a wooden board (for simplicity further on called closed containers), so that only mosquitoes could gain access to the water; the remaining 25 containers were left uncovered (open containers) so that they could be colonized by both mosquitoes and Odonates. Such containers are used in most rural homes and farmlands in the tropics for harvesting rain water and/or storing water for domestic use and irrigation (Rämi, 2003; Nega, 2005; Amha, 2008). When filled with water, these containers usually serve as a breeding ground for mosquitoes (Waktola, 2008). The containers were left for two weeks to allow colonization by mosquitoes and Odonates. Colonization of open containers by Odonates was determined by observing the territorial behaviour of males and oviposition by females, and the presence of larvae and eventually exuviae from emerging adults. The density of mosquito larvae in each container was assessed weekly for an additional eight weeks by counting the number of larvae in six samples scooped with a 1/,L beaker (see Mandal et al., 2008). The water level in each container was maintained by adding groundwater as necessary. At the end of the 10 weeks, 45 Odonate larvae were collected from colonized open containers and reared in the laboratory with temperature varying between 24 and 32 ºC. Odonate larvae were kept individually in small plastic containers with a height 9 cm and base diameter of 9 cm half-filled with pond water (Figure S4.1). A stick was placed in each plastic container to support adult emergence. Odonate larvae were fed on mosquito larvae until emergence and adults were identified according to Dijkstra and Clausnitzer (2014).

4.3.3 Data analysis

All analyses were conducted in R version 3.3.2 software (R Development Core Team, 2016). To manipulate and organize the data, the package *tidyr* was used (Wickham, 2017). To analyse the impact of shade, container type, and time since start of the experiment on the number of mosquito larvae, we fitted generalized mixed-effects models using distributions appropriate for count data (Poisson, negative binomial; Hadfield, 2010; Table S4.1). As fixed effects, we fitted the factors *container* (open or closed), *shade* (shaded or sunlit) and within the factor *container* the continuous variable *day* (i.e. time from the start of the experiment). This procedure was necessary as we expected that the change in population density of the mosquito larvae differs between open containers (decreases with time, owing to predation) and closed containers (no change with time). Furthermore, we included a random slope for each container as well as a random intercept for each *count* (repeated count of mosquito larvae with each scoop). The random factors account for any variations that might exist between experimental containers as a result of varying microhabitat conditions and also account for the repeated counts (see model details in Tables 4.2, S4.1, S4.2). When a Poisson-distribution was used, model 1 showed signs of over-dispersion; therefore, we included a random effect of individual level variability to account for over-dispersion (Model 2a). However, model 2a failed to converge; therefore, we used other functions as well as error distributions to test whether the estimates were robust (Tables S4.1, S4.2). Overall, we tested nine models but since all models produced similar results (Tables S4.1, S4.3, Figure S4.2), we present results of the reduced model 2d (results of other models are presented in Table S4.2). Using the *model.sel* function (Barton, 2015) in the R-package *MuMln*, model 2d was the best selected from the converging models (Table S4.3).

4.4 RESULTS

Mosquitoes (Aedes, Culex) began to colonize the containers a week after the start of the experiment. Colonization of the containers by Odonates also commenced at this time with the incidence of an ovipositing female *Bradinopyga strachani* (Family Libellulidae). By the third week after the start of the experiment, 21 (84 %) of the open containers were colonized by Odonate larvae; all 14 open containers in sunlit areas and 7 in shaded areas. Although five dragonfly species were observed within the study area (*Palpopleura lucia*, *Pantala flavescens*, *Bradinopyga strachani*, *Tramea basilaris*, and *Orthetrum austeni*), only B. strachani colonized the containers. Both *B. strachani* and *O. austeni* successfully bred in an older irrigation pond within the study area; no mosquito larvae were recorded in this pond. Shade of the breeding site positively influenced the density of mosquito larvae (Tables 4.2, S4.2). Our results indicated also that density of mosquito larvae in open containers were lower (possible presence of dragonfly larvae) compared to closed containers. Furthermore, particularly in open containers, density of mosquito larvae decreased with the time since start of the experiment (indirect variable describing the maximum possible age of Odonate larvae (Tables 4.2, S4.2).

Table 4.1 | List of studies on predator-prey interactions between mosquito larvae and various lineages of predators.

Predator lineage	References
Crustaceans	Kay et al., 1992; Marten et al., 1994; Kumar and Rao, 2003; Panogadia-Reyes et al., 2004; Martin and Reid, 2007.
Nematodes	Mijares et al., 1999; Perez-Pacheco and Flores, 2005.
Fish	Neng et al., 1987; Blaustein and Byard, 1993; Wang, 1998; Hammer et al., 2002; Mohamed, 2003; Chandra et al., 2008.
Hemipterans	Aditya et al., 2004; Saha et al., 2007; Sivagnaname, 2009.
Amphibians	Komak and Crossland, 2000; Mokany and Shine, 2003; Raghavendra et al., 2008.
Coleopterans	Lundkvist et al., 2003, Aditya et al., 2004; Aditya et al., 2006.
Heteropterans	Rodriguez-Castro et al., 2006; Saha et al., 2007.
Dipterans	Hechtel and Juliano, 1997; Aditya et al., 2007; Nyamah et al., 2011.
Odonates	**Mathavan, 1976**; **Sebastian et al., 1980**; **Muira and Takahashi, 1988**; Sebastian et al., 1990; Fincke et al., 1997; **Stav et al., 2000**; **Singh et al., 2003**; **Quiroz-Martinez et al., 2005**; **Stav et al., 2005**; Chatterjee et al., 2007; **Mandal et al., 2008**; **Saha et al., 2009**; Sathe and Bhusner, 2010; **Kweka et al., 2011**; **Saha et al., 2012**; **Venkatesh and Tyagi, 2013a, 2013b; Wetterings et al., 2015; Jacob et al., 2017.**

The listed studies involved organisms that could potentially colonize mosquito breeding habits and are able to reproduce in these habitats, and pose no danger to people (Bellows, 2001; Headrick and Goeden, 2001; Spielman et al., 1993; see reviews in Quiroz-Martinez and Rodriguez-Castro, 2007 and Kumar and Hwang, 2006). Many of the studies involving Odonates were laboratory-based and/or made use of starved predators (citations in bold).

Table 4.2 | Summary of model estimates (± standard errors SE). We also give the equations for the three models using the formalism of R (R Development Core Team, 2016).

	Model 1	Model 2a	Model 2d
Intercept ± SE	–0.01 ± 0.80	–0.40 ± 0.76	–0.34 ± 0.15
Open Containers ± SE	–2.71 ± 0.97	–2.67 ± 0.90	–1.61 ± 0.15
Shaded ± SE	0.96 ± 0.27	0.75 ± 0.42	0.53 ± 0.13
Open Container : day ± SE	–1.33 ± 0.40	–1.22 ± 0.42	–0.36 ± 0.08
AIC	4099.7	3348.1	3583.6

Model 1: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | count)

Model 2a: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | count) + (1 | obs)

Model 2d: number of larvae ~ container + container : day + shade + (1 | obs)

The factor *container* has two levels (open and closed), the factor *shade* also has two levels (shaded and sunlit), *day* is a continuous variables and measures the time since the start of experiment(thereby also an indirect variable for the age of larvae), *count* refers to repeated counts of mosquito larvae, *obs* refers to the observations of each individual container, *code* refers to the codes given to each experimental container, (*1* | *count*) indicates a random intercept of the repeated counts, (*1* | *obs*) the random intercept for each observation, and (*1* + *day* | *code*) random slope for each container. For each model we also give the Akaike information criterion (AIC).

4.5 DISCUSSION

Our study investigated whether and, if so, which Odonates co-occur with mosquitoes in semi-natural systems, whether Odonates colonize mosquito breeding sites of low habitat quality, and whether the presence of Odonate larvae leads to a decrease in the density of mosquito larvae. Our results indirectly assess the potential of dragonfly and damselfly larvae for the biological control of mosquito larvae.

Although an earlier inventory of Odonates on the University of Ghana Legon campus by Acquah-Lamptey et al. (2013b) reported 26 species, we recorded only 5 species during the current study. *Bradinopyga strachani* was the only species that successfully colonized the experimental containers. This is not surprising as this species, which is also known as a “rock dweller”, often breeds in rock pools and open water tanks. The distributional range of B. strachani spans from western Kenya to Guinea and Mali (Clausnitzer and Dijkstra, 2016) covering about a quarter of the area in Africa with malaria (Figure S3). The species has also been recorded close to villages. Species of the genus Bradinopyga are successful predators of mosquitoes (Venkatesh and Tyagi, 2013a; Varshini and Kanagapapan, 2014), but Sebastian et al. (1990) argued that *B. geminata* would not be appropriate for mosquito control because it cannot be easily reared to the adult stage in captivity. This argument does not hold for B. strachani, as all 45 larvae collected from the containers survived in the laboratory until emergence as adults. Nevertheless, we want to stress that our aim was not to show that artificial rearing of Odonates can be used to multiply potential agents for biological control. We only wanted to show that under natural conditions some Odonates colonize artificial containers and that in such containers these Odonates reduce the density of mosquito larvae.

In Accra (Ghana), species of Culex, Aedes, and Anopheles can coexist in the same breeding sites, with Culex dominating the mosquito assemblages (Brown et al., 2014). Although it has been reported that Anopheles mosquitoes breed in open, clear, and sunlit pools (Opoku et al., 2007) and *Anopheles gambiae* larvae develop in permanent, man-made concrete tanks (Mala et al., 2011), we did not find any larvae of this genus in our experimental containers. This absence could be explained by a preference of Anopheles for water bodies close to human dwellings, as observed in Senegal during the rainy season (Diédhiou et al., 2016), as well as the preference of females for black-bottomed habitats and pools with muddy and non-vegetated edges for oviposition (McCrae, 1983; Huang et al., 2005).

The development of *B. strachani* in open containers resulted in a significant decrease in the number of mosquito larvae (Table 4.2). A significant reduction of mosquito density results from the interaction effect between open containers and time since the start of the experiment (variable day). As *B. strachani* increases in size with time, predation increases leading to a further reduction in mosquito density (Figure S4.5). This is in accordance with the observation of Weterings et al. (2015) that the predation rates of Odonates increase with body size. Our study does not support the postulates of Sebastian et al. (1990) that it is unlikely that dragonflies and mosquito coexist naturally and that Odonates would not be selective enough in their feeding to decrease densities of mosquito populations. Several studies have concluded that dragonflies are active predators of mosquitoes (e.g. Fincke et al., 1997; Quiroz-Martinez et al., 2005; Stav et al., 2005; Chatterjee et al., 2007; Mandal et al., 2008; Saha et al., 2009; Sathe and Bhusner, 2010; Kweka et al., 2011) and our field experiment supports these reports. Although this conclusion is mostly based on laboratory studies, the results of our study indicate that the natural co-occurrence of the predator offers an inexpensive complementary approach for managing mosquito densities. In our opinion, the most inexpensive method is to promote the natural occurrence of Odonates. One referee suggested that even adult Odonates might contribute to the reduction of mosquitoes by feeding on adult mosquitoes. In general, the diet of adult Odonates is very diverse

(Sukhacheva, 1996). For example, out of 41 individual wild-caught adult Odonates belonging to five species, only four individuals belonging to two species had traces of mosquito remnants in the gut (Pfitzner et al., 2015). Therefore, we expect that adult Odonates have little influence on the population size of adult mosquitoes.

The reduction in the density of mosquito larvae in closed containers without predators (Fig. S5) could be due to density-dependent competition (Agnew et al., 2002; Roberts and Kokkinn, 2010; Yoshioka et al., 2012). Density dependent competition decreases growth rates of larvae, increases larval mortality, delays pupation, and results in the emergence of smaller adults. A study of predation of *Bradinopyga geminata* larvae on mosquito larvae in a laboratory experiment in India has shown that this species has a stronger preference for larvae of Culex and Aedes species than for those of Anopheles (Venkatesh and Tyagi, 2013a), which is keeping with the bottom-feeding behaviour of both Odonate larvae (Corbet, 1980) and Aedes larvae (Bay, 1974). Although Aedes larvae alter their feeding behaviour in the presence of predators that pose a high risk (Roberts, 2014). Thereby larvae of Aedes switch from bottom feeding to less efficient surface filter feeding (Roberts, 2012). The larvae of *Culex quinquefasciatus*, by contrast, easily become habituated to the presence of predators (Roberts, 2014).

Shade had a significant positive effect on the density of mosquito larvae, which suggests that microclimate could play a vital role in the success of a natural bio-control programme. First of all, shade could have an adverse effect on the colonization of water bodies by dragonflies (Clark and Samways, 1996; Samways et al., 2005; Remsburg et al., 2008). We observed that adult male dragonflies basked on sunlit containers and defended sunlit containers from other males more than shaded containers. Secondly, shading might result in a reduction of water temperature to the optimum for the survival of mosquito larvae (Vezzani and Albicócco, 2009; Wamae et al., 2010; Mala et al., 2011; Rubio et al., 2011).

High water temperatures decrease the survival of mosquito larvae (Christiansen-Jucht et al., 2014). Altogether, this suggests that exposing water-storage containers to sunlight in mosquito-prone regions would increase mortality of mosquito larvae as well as predation (see Christiansen-Jucht et al., 2014). Although covering containers with a fine mesh is the most effective way to keep out mosquitoes, in remote and poor areas where material for covering the containers is not available, keeping the containers in the sun is a cheap possibility to control mosquitoes.

4.6 CONCLUSIONS

Although it is believed that Odonate larvae do not naturally coexist at high densities with mosquito larvae, and that these predators are not selective enough in their feeding to reduce the density of mosquito larvae, the result of our study showed that *B. strachani* larvae are able to reduce densities of mosquito larvae under semi-natural conditions. This species, which is common around households, has shown its ability to easily breed in water storage containers, which also serve as mosquito breeding reservoirs. Though total covering of water-storage containers is ideal to prevent mosquitoes from breeding in such containers, keeping water-storage containers in sunlit areas to increase water temperature to hinder the development of mosquito larvae and to allow the colonization by *B. strachani* would be promising for suppressing mosquito-borne diseases by vector control in cases where covering of containers is not possible. Promoting the use of such naturally occurring biological control agents of mosquitoes in rural communities would ensure the reduction of pesticide use, savings on pesticide costs, reduced risk of chemical residues on farm products and households, and a safer environment.

PART III – SYNTHESIS, APPLICATION, AND OUTLOOK

CHAPTER FIVE

5.0 SYNTHESIS

1) Temperature-driven colour lightness and body size variation scale to local assemblages of European dragonflies but are modified by propensity for dispersal

Environmental temperature is one of the most important environmental factors influencing the distribution of ectotherms (Pinkert et al., 2018). Temperature affects many fundamental physiological functions and life-history traits of ectotherms (Angilleta et al., 2002). Thermodynamically functional traits such as colour and body size directly link to heat gain or loss of an organism's body temperature (Clusella-Trullas et al., 2007; Shelomi, 2012).

Our findings from this thesis showed that the spatial variation in colour lightness and body size of European Odonates is driven mainly by temperature (Chapter 2). Our continent-wide yet spatially explicit assessment of these relationships reconciles with previous macroecological (e.g. Pinkert et al., 2017; Zeuss et al., 2014, 2017) and experimental (e.g. May, 1991; Samejima & Tsubaki, 2010) evidence. This indicates the general importance of the mechanistic links of colour lightness and body size with the temperature regime which shapes the biogeographical patterns of Odonates. The colour lightness-temperature relationship was consistent with the predictions of the thermal melanism hypothesis. Furthermore, consistent with Bergmann's rule *sensu lato*, we found that the average body size of assemblages of Odonates decreased with increasing temperature.

The overall geographical patterns in the colour lightness and body volume of assemblages of Odonates were consistently driven by both temperature and annual precipitation. However, we found that lotic assemblages in regions of lower precipitation were on average smaller than those in humid regions. This suggests an additional advantage of higher size-based desiccation tolerance. This constrains their ability to thermoregulate via body size. Furthermore, we showed that species adapted to lotic habitats were significantly larger in regions that are both warm and wet. This finding supports the predictions of

Gloger's rule (Wilson et al., 2001), which have been generally strongly supported by several large-scale studies (Pinkert et al., 2017; Stelbrink et al., 2019; Zeuss et al., 2014).

2) Extrinsic environmental traits modulate the relationship between intrinsic functional traits and the extinction risk of European and African Odonata

Using a generalized ecophysiological framework, we show how ecological mechanisms such as relationships of habitat stability and dispersal with range size and maximum latitude, as well as body size with maximum latitude and temperature preference translate into extinction risk. Having argued that species ranges are generally only available for a small proportion of taxa (Jeliazkov et al., 2022) and studies of extrinsic drivers of extinction risk lack explanations of why some species are more threatened than others – an understanding that is essential to mitigate extinction risk through targeted management, our results generally support strong direct effects of the range size and species latitudinal limit (species maximum latitude) on species extinction risk documented in previous studies.

Secondly, our results provide the first evidence for several trait-environment relationships across an entire latitudinal gradient that thus far, only have been investigated for temperate insect taxa, including the temperature-size rule and Bergmann's rule. We also show that body size which is frequently used in analyses of species' extinction risk yields ambiguous and most often non-significant effects (Chichorro et al., 2019). We argue that part of this heterogeneity is explained by the confounding effects of wing load and the thermoregulatory importance of body size (Pinkert et al., 2020a). We suggest that despite the physiological evidence for higher cost for dispersal or mobility of species with a larger body relative to their wing size, the use of body size as a proxy for the dispersal ability may lead to misinterpretations of the role of dispersal versus thermoregulation. We also show that species adapted to lentic (less stable) habitats have a lower risk of extinction than those adapted to lotic (stable) habitats. This strong and consistent effect of habitat preference on range size and ultimately on extinction risk may therefore explain previous support for a lower threat of lentic species compared to lotic species (Korkeamäki & Suhonen, 2002; Rocha-Ortega et al., 2019).

Based on our findings and support from previous studies, we recommend conservation efforts targeted at improving the water quality of rivers and streams. Furthermore, our results highlight that cold-adapted (i.e. large and in high latitude) with a poor dispersal ability (i.e. high wing load and small range) and propensity (i.e. lotic and small range) are more threatened. Since most of the considered traits carry strong phylogenetic signals, climatic changes, and consequent responses, would threaten lineages that have such characteristics.

3) Effect of a dragonfly (*Bradinopyga strachani* Kirby, 1900) on the density of mosquito larvae in a field experiment using mesocosms

Among the various lineages of predators used as biological control agents (Table 3.1), Odonates have shown outstanding ability and efficacy especially at the larval stages (e.g., Sebastian et al., 1990; Lubelczyk et al., 2020). Despite this, the argument remains that Odonates do not share the same breeding habitats and may not be naturally selective enough to control the targeted pest population (Service, 1977; Collins et al., 2019).

We have confirmed that Odonates and mosquitoes share artificial habitats in space and in time. As opposed to the introduction and augmenting efforts (Sebastian et al., 1990; Lubelczyk et al., 2020), the widespread tropical dragonfly B*radinopyga strachani* colonized typical water-storage containers used in many African villages and was able to reduce the larval density of *Aedes* and *Culex* mosquitoes. Leaving large storage containers or reservoirs wide open encourages the colonisation and breeding of Odonates which actively prey on mosquitoes breeding in such containers. This is indeed an effortless and promising approach to suppressing mosquito-borne diseases by vector control, especially in poor rural areas where water is harvested and stored in artificial containers.

5.1 APPLICATION

Understanding the physiological processes shaping species distribution and composition is not only theoretically important, but it also has important implications for biodiversity conservation as it affects species vulnerability. For instance, species with low dispersal ability have significantly smaller geographical ranges (e.g., Juliano, 1983) and hence are more vulnerable to extinction, especially from habitat loss (Staude et al., 2019). Therefore, associating a species' functional traits with its climatic environment is important to understand the drivers of species distributions and the variations in species range sizes. This is essential to predict the effect or consequences of climate change on species distribution and extinction risk.

We show that Odonata assemblages in colder climates are bigger and darker. Therefore, we suggest that as a response to global warming, they will become smaller and lighter on average (Chapter 2). Also, we provide the first evidence for the temperature-size rule that previously has only been investigated for temperate insect taxa, that body size of European and African Odonates decreases with increasing temperature (Chapter 3).

Our results show that the mechanism underlying colour lightness and body size variations were of equal evolutionary significance for lentic and lotic species. However, higher dispersal ability enables lentic species to cope better with historical climatic changes. Similarly, in line with the predictions of the habitat-stability hypothesis and previous findings on freshwater organisms in temperate regions (Hof et al., 2006; Grewe et al., 2013), we show that species adapted to lentic habitats generally have a larger range size and hence a lower risk of extinction (Chapter 3). Thus, lotic water species are more threatened with extinction because of a lower capacity to cope with environmental changes compared to lentic species.

We highlight the importance of species traits and our support for inferences drawn from the direct effects of species functional traits on their distribution and risk of extinction.

However, our results suggest that the trait-environment relationships are complex. For instance, species with lower wing loads generally have larger range sizes and, therefore, a reduced extinction risk, whereas species with a lower wing load occur at higher latitudes where species have an increased extinction risk. Similarly, larger species occur at higher latitudes where species have an increased risk of extinction. These propose that multiple trait-environment relationships determine a species' ecological dynamics and threat status in concert.

In total, we highlight the importance of integrating species dispersal ability and morphological traits into mechanistic models to significantly improve the accuracy of predicting species distribution and extinction risk assessments. Species trait information is readily available for many species and they could serve as important substitutes for range maps as trait-based analyses enhance the efficiency of conservation assessments, and the understanding of the mechanisms underlying species distribution and composition especially when not many invertebrates have been assessed and a good fraction of these species lack range maps.

In addition, we highlight the ability of a common widespread dragonfly *Bradinopyga strachani* to colonise water storage containers used in rural communities which serve as reservoirs for mosquitoes. The presence of the Odonate resulted in the drastic reduction of the mosquito larval density (Chapter 4). In practicality, rural communities that store water in such concrete containers once aware would promote the conditions for Odonates to colonise these containers to reduce the mosquito larval densities. Since these containers are partially covered such that mosquitoes can manoeuvre into them to breed, we recommend that the containers are left wide open. This promotes the incidence of sun rays on the containers. This may increase the water temperature, making it unfavourable for mosquito breeding but also favourable for Odonates to breed in them.

5.2 OUTLOOK

The syntheses of my findings highlight several advantages of Odonata in macro-ecological studies. As model organisms, studying the interactions between the functional traits and Odonate's environment helps to understand the mechanisms associated with these interactions. With increased availability of data on functional traits coupled with advanced ecological modelling (especially trait-based models), there is thus the possibility to improve our understanding of the variations in species distributions and composition. This is also vital in conservation ecology as involving functional traits, species dispersal ability in ecological models with the species' climatic environment, improves our understanding of why some species may be more threatened than others and the underlying mechanisms responsible.

The findings of my thesis highlight the crucial role of the thermoregulatory traits in shaping the distribution of Odonates even at the local assemblage level, confirming the robustness of studies using expert range maps. Odonata assemblages in warmer regions were consistently smaller and lighter coloured than assemblages in cooler regions. Firstly, an increase in body size results in the reduction of the surface area to volume ratio such that large bodies retain heat more efficiently than smaller bodies (Shelomi, 2012). Secondly, melanization of the cuticle affects heat gain or loss, a mechanism referred to as thermal melanism (Clusella-Trullas et al., 2007). Besides thermoregulation, greater melanisation increases resistance against pathogens, by enhancing the structural integrity of cells (Gloger's rule, Rapoport, 1969). Under xeric conditions, a larger body size is advantageous since its lower surface area to volume ratio reduces water loss through the cuticle (Kühsel et al., 2017). Furthermore, lentic and lotic assemblages of odonates demonstrated varied strength and relative importance of the climatic drivers of colour lightness and body size. Thus supporting the claim that dispersal propensity coupled in habitat preference, and thermal sensitivity affects a species' capability to cope with environmental changes.

Due to both the lack of experts and the time-consuming process of generating species range maps that form the basis of species threat assessment, a large majority of taxa remain unassessed or classified as data deficient. We show that by integrative modelling approaches that use readily available trait information combined with estimates of the species distribution and climatic requirements, has a high potential of providing initial outcomes of species risk assessments. Also, coupled with further intrinsic, extrinsic traits, and the phylogenetic relationship of species can serve to refine the outcome of this ecophysiological framework analysis. Based on our findings, we suggest that species limited both in their dispersal ability, dispersal propensity, as well as geographical barriers (i.e. shifts impossible if species are already at the mountain tops) have higher risk of extinction. Targeted conservation may thus focus on improving habitat conditions especially, rivers and streams, connect populations with habitat steppingstones, or even assist species' migration.

In most Odonate-mosquito control programs, the Odonate larvae are introduced into the mosquito habitats (Lubelczyk et al., 2020). We have demonstrated that a widespread dragonfly species *Bradinopyga strachani* can colonise mosquito breeding habitats and actively reduce their population density contrary to the expected. In most rural homes, water storage containers serve as breeding grounds for mosquitoes. These containers are not well covered or placed in shaded areas. We show that leaving these containers open in sunlit areas attracts Odonates who can actively control mosquito larvae. A limitation to the success of this effortless and promising mosquito larvae control method, even in cases where augmentation is done, is the human factor that makes it successful. We therefore recommend increased awareness of insect biodiversity expecially in Africa (see other manuscripts in the appendix).

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APPENDICES

SUPPORTING INFORMATION

Appendix 1 Temperature-driven colour lightness and body size variation scale to local assemblage of European dragonflies but are modified by dispersal.

Appendix 2 Extrinsic environmental traits modulate the relationship between intrinsic functional traits and the extinction risk of European and African Odonata.

Appendix 3 Effect of a dragonfly (Bradinopyga strachani Kirby, 1900) on the density of mosquito larvae in a field experiment using mesocosms

Appendix 1

TEMPERATURE–DRIVEN COLOUR LIGHTNESS AND BODY SIZE VARIATION SCALE TO LOCAL ASSEMBLAGES OF EUROPEAN DRAGONFLIES BUT ARE MODIFIED BY DISPERSAL

Daniel Acquah-Lamptey, Martin Brändle, Roland Brandl**,** Stefan Pinkert

Supporting information for manuscript 2.1

2.1 | Data sources

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TABLE S2.1 | Variable contributions of principal component analysis based on the correlation of 19 commonly used temperature and precipitation variables calculated using the *prcomp* function of the R-package *stats*. Bioclimatic variables used in the analysis were extracted from climate data with a resolution of 2.5 arcminutes (retrieved from www.chelsa-climate.org; Karger et al., 2017; Karger et al., 2018), based on the geographical coordinates of dragonfly assemblages (with a buffer radius of ~1 km). Variable contributions were calculated by singular value decomposition of the (centred and scaled) data matrix.

	Temperature		Precipitation	
Bioclimatic variables	PC 1	PC 2	PC 1	PC 2
Annual mean temperature	11.62	9.45		
Mean diurnal temperature	9.07	11.79		
Isothermality	0.01	1.81		
Temperature seasonality	8.83	10.64		
Max temperature of warmest month	1.93	32.68		
Min temperature of coldest month	15.09	0.28		
Temperature annual range	11.69	8.02		
Mean temperature of wettest quarter	5.77	8.19		
Mean temperature of driest quarter	12.81	0.03		
Mean temperature of warmest quarter	8.48	15.29		
Mean temperature of coldest quarter	14.71	1.81		
Annual precipitation			24.57	0.82
Precipitation of wettest month			22.08	2.9
Precipitation of driest month			3.32	26.13
Precipitation seasonality			0.16	25.54
Precipitation of wettest quarter			22.22	2.89
Precipitation of driest quarter			7.49	20.79
Precipitation of warmest quarter			0.25	19.07
Precipitation of coldest quarter			19.89	1.83
Eigenvalues	6.34	2.59	3.83	3.28
Standard deviation	2.52	1.61	1.96	1.81
proportion of variance	57.64	23.53	47.86	41.06
Cumulative proportion of variance	57.64	81.17	47.86	88.92

TABLE S2.2 | Variance inflation factors of predictor variables from multiple regression models (in Tables 1 and 2) of average colour lightness and body volume of European dragonfly assemblages (both = 518, lentic = 337, lotic = 181) with z-standardized temperature and precipitation variables.

Predictors	Both	Lentic	Lotic	Interaction
Annual mean temperature	1.63	1.58	2.60	1.40
Temperature seasonality	1.20	1.22	1.52	1.13
Annual precipitation	1.20	1.09	1.76	1.18
Precipitation seasonality	1.34	1.43	1.25	1.16

TABLE S2.3 | Effect sizes (z-scores) and the explained variance of predictor variables from single and multiple regressions (r^2/R^2) of the average, species-specific and phylogenetic components of the average colour lightness and body volume of 337 lentic and 181 lotic assemblages of European odonates with z-standardized temperature and precipitation variables. In addition, regression models (Nagelkerke pseudo-r^2/R^2) calculated with a spatial dependency weight are given. Significant relationships ($p < 0.05$) are shown in bold. The predictors are: annual mean temperature (AMT), and annual precipitation (AP). The P - component represents the phylogenetically predicted part of the respective trait and S - component represents the respective deviation of the average trait from the P - component.

				Average				S - component				P - component			
				Lentic		Lotic		Lentic		Lotic		Lentic		Lotic	
Model		Trait	Predictor	Z-score	r^2/R^2	Z-score	r^2/R^2	Z-score	r^2/R^2	Z-score	r^2/R^2	Z-score	r^2/R^2	Z-score	r^2/R^2
Ordinary least-squares regression	Single	Colour lightness	AMT	**10.97**	0.26	**7.44**	0.24	**10.01**	0.23	**3.91**	0.08	**9.49**	0.21	**6.45**	0.19
			AP	0.85	0.00	**5.73**	0.20	0.49	0.00	**3.54**	0.07	–0.02	0.00	**3.22**	0.06
		Body volume	AMT	**–2.51**	0.02	**2.12**	0.03	–1.26	0.00	**–2.8**	0.04	**–2.45**	0.02	**2.36**	0.03
			AP	0.88	0.00	**3.53**	0.06	1.94	0.01	**–2.53**	0.03	0.93	0.00	**3.85**	0.08
	Multiple	Colour lightness	AMT	**9.5**		**5.45**		**9.98**		**2.22**		**9.5**		**5.45**	0.19
			AP	–0.64	0.21	–0.54	0.19	–0.09	0.23	1.51	0.09	–0.64	0.21	–0.54	
		Body volume	AMT	**–2.52**		0.11		–1.39		–1.58		**–2.52**		0.11	0.08
			AP	1.1	0.02	**2.99**	0.08	2.03	0.02	–1.07	0.05	1.1	0.02	**2.99**	
Spatial autoregressive error	Single	Colour lightness	AMT	**10.25**	0.28	**4.56**	0.28	**10.04**	0.23	**2.46**	0.12	**9.2**	0.26	**6.39**	0.19
			AP	0.57	0.06	**2.73**	0.23	–0.05	0.05	1.92	0.11	0.13	0.07	1.28	0.08
		Body volume	AMT	**–2.5**	0.03	1.29	0.03	–1.07	0.01	**–2.92**	0.04	**–2.45**	0.03	1.3	0.04
			AP	0.97	0.02	**3.15**	0.07	**2.68**	0.03	**–2.48**	0.03	1.02	0.02	**3.3**	0.08
	Multiple	Colour lightness	AMT	**10.21**		**3.71**		**10.04**		1.83		**9.22**		**5.4**	0.19
			AP	1.04	0.28	1.26	0.28	–0.10	0.23	1.04	0.12	0.68	0.26	–0.56	
		Body volume	AMT	**–2.48**		–0.03		–0.96		–1.61	0.05	**–2.43**		–0.02	0.08
			AP	0.93	0.04	**2.65**	0.07	**2.61**	0.03	–1.07		0.96	0.04	**2.81**	

TABLE S2.4 | Individual slopes and standard error (SE) of predictor variables from single regression (r^2) of the average, species-specific and phylogenetic components of the average colour lightness and body volume of 337 lentic and 181 lotic assemblages of European odonates with z-standardised environmental variables. In addition, regression models (Nagelkerke pseudo-r^2) calculated with a spatial dependency weight are given. Shaded cells indicate significant differences in the slopes of these regressions between lotic and lentic assemblages. Slopes that are significant from zero ($p < 0.05$) are shown in bold. The predictors are: annual mean temperature (AMT); and annual precipitation (AP). The P - component represents the phylogenetically predicted part of the trait and S - component represents the respective deviation of the average trait from the P - component.

Model	Trait	Component	Predictor	Slope ± SE for lentic	Slope ± SE for lotic	r^2
Ordinary least-square regression	Colour lightness	Average	AMT	**$3.0 \times 10^{0} \pm 2.8 \times 10^{-1}$**	**$3.3 \times 10^{0} \pm 3.5 \times 10^{-1}$**	0.28
		S - component	AMT	**$1.2 \times 10^{0} \pm 1.2 \times 10^{-1}$**	**$8.2 \times 10^{-1} \pm 1.5 \times 10^{-1}$**	0.21
		P - component	AMT	**$1.5 \times 10^{0} \pm 1.7 \times 10^{-1}$**	**$1.6 \times 10^{0} \pm 2.1 \times 10^{-1}$**	0.22
		Average	AP	$3.8 \times 10^{-1} \pm 3.3 \times 10^{-1}$	**$2.5 \times 10^{0} \pm 3.8 \times 10^{-1}$**	0.08
		S - component	AP	$1.3 \times 10^{-1} \pm 1.4 \times 10^{-1}$	**$6.6 \times 10^{-1} \pm 1.6 \times 10^{-1}$**	0.03
		P - component	AP	$2.6 \times 10^{-2} \pm 1.9 \times 10^{-1}$	**$8.5 \times 10^{-1} \pm 2.2 \times 10^{-1}$**	0.03
	Body volume	Average	AMT	**$-2.4 \times 10^{-2} \pm 8.3 \times 10^{-3}$**	$1.1 \times 10^{-2} \pm 1.0 \times 10^{-2}$	0.02
		S - component	AMT	$-9.1 \times 10^{-5} \pm 6.4 \times 10^{-5}$	**$-2.3 \times 10^{-4} \pm 7.9 \times 10^{-5}$**	0.02
		P - component	AMT	**$-2.4 \times 10^{-2} \pm 8.4 \times 10^{-3}$**	$1.4 \times 10^{-2} \pm 1.0 \times 10^{-2}$	0.02
		Average	AP	$4.4 \times 10^{-3} \pm 8.5 \times 10^{-3}$	**$2.8 \times 10^{-2} \pm 9.9 \times 10^{-3}$**	0.02
		S - component	AP	$1.3 \times 10^{-4} \pm 6.5 \times 10^{-5}$	**$2.0 \times 10^{-4} \pm 7.5 \times 10^{-5}$**	0.02
		P - component	AP	$4.9 \times 10^{-3} \pm 8.6 \times 10^{-3}$	**$3.2 \times 10^{0} \pm 9.9 \times 10^{-3}$**	0.02
Spatial autoregressive error models	Colour lightness	Average	AMT	**$2.1 \times 10^{1} \pm 2.1 \times 10^{0}$**	**$2.5 \times 10^{1} \pm 2.0 \times 10^{0}$**	0.33
		S - component	AMT	**$6.9 \times 10^{0} \pm 8.6 \times 10^{-1}$**	**$8.9 \times 10^{0} \pm 8.1 \times 10^{-1}$**	0.25
		P - component	AMT	**$1.3 \times 10^{1} \pm 1.3 \times 10^{0}$**	**$1.3 \times 10^{1} \pm 1.2 \times 10^{0}$**	0.24
		Average	AP	**$2.1 \times 10^{0} \pm 1.5 \times 10^{0}$**	**$4.9 \times 10^{0} \pm 1.7 \times 10^{0}$**	0.15
		S - component	AP	$9.4 \times 10^{-1} \pm 6.1 \times 10^{-1}$	$4.6 \times 10^{-1} \pm 7.2 \times 10^{-1}$	0.09
		P - component	AP	$2.0 \times 10^{-1} \pm 8.6 \times 10^{-1}$	$1.8 \times 10^{0} \pm 1.0 \times 10^{0}$	0.08
	Body volume	Average	AMT	$-3.5 \times 10^{-2} \pm 6.1 \times 10^{-2}$	**$-1.4 \times 10^{-1} \pm 5.9 \times 10^{-2}$**	0.05
		S - component	AMT	**$-8.9 \times 10^{-4} \pm 4.5 \times 10^{-4}$**	**$-1.2 \times 10^{-3} \pm 4.3 \times 10^{-4}$**	0.02
		P - component	AMT	$-2.9 \times 10^{-2} \pm 6.2 \times 10^{-2}$	**$-1.3 \times 10^{-1} \pm 6.0 \times 10^{-2}$**	0.02
		Average	AP	$5.6 \times 10^{-3} \pm 3.7 \times 10^{-2}$	**$1.6 \times 10^{-1} \pm 4.4 \times 10^{-2}$**	0.05
		S - component	AP	**$6.8 \times 10^{-4} \pm 2.9 \times 10^{-4}$**	$-4.9 \times 10^{-4} \pm 3.4 \times 10^{-4}$	0.03
		P - component	AP	$8.1 \times 10^{-3} \pm 3.7 \times 10^{-2}$	**$1.8 \times 10^{-1} \pm 4.4 \times 10^{-2}$**	0.05

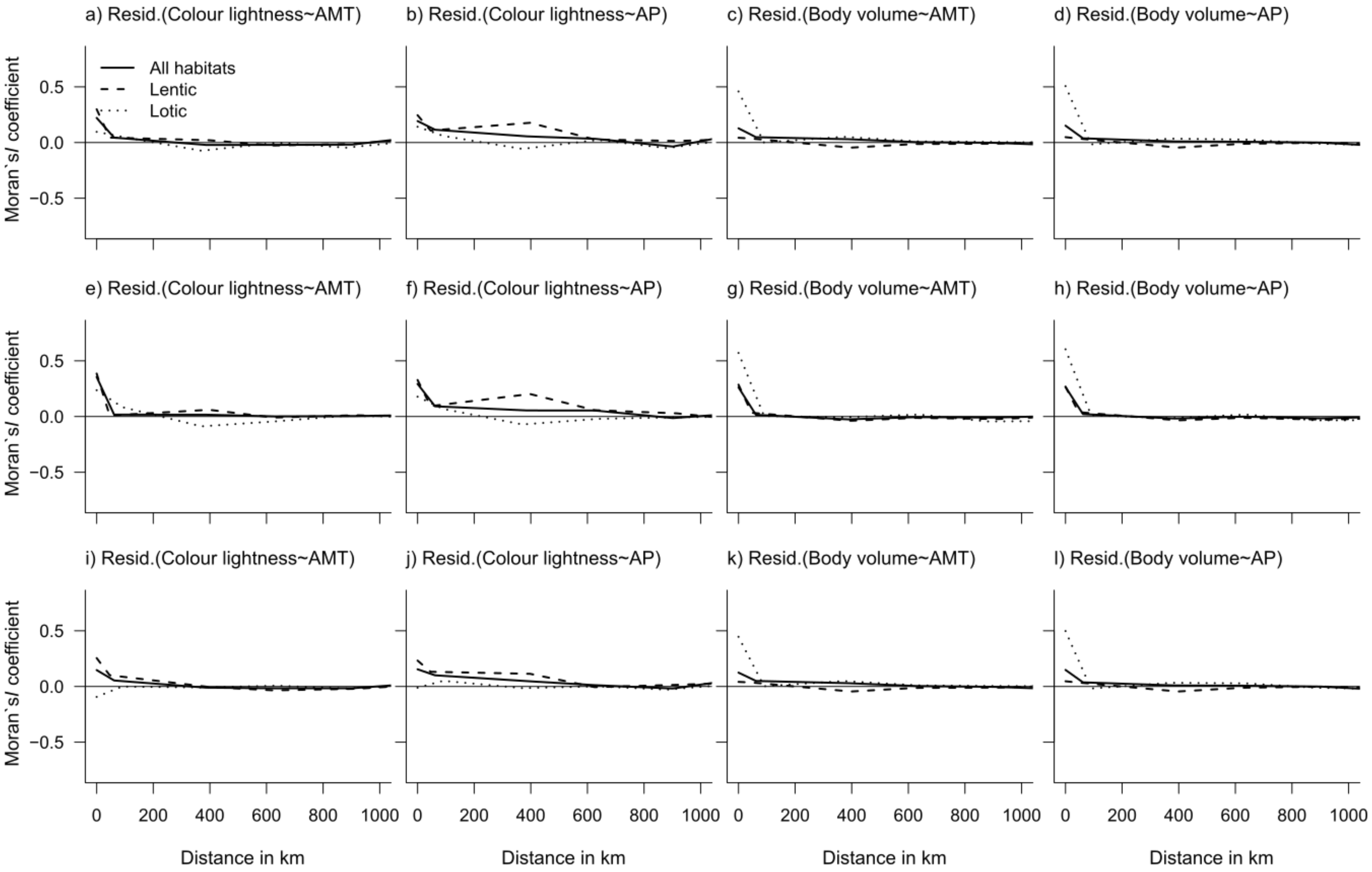

FIGURE S2.1 | Spatial correlogram of Moran's *I* coefficient of the residuals from the single regression model of the average, species-specific and phylogenetic components of the average colour lightness and body volume of assemblages of European odonates (all habitats = 518, lentic = 337, lotic = 181) with z-standardized temperature and precipitation variables. The abscissa is distance classes of assemblages and the ordinate is Moran's *I* coefficients where a value of zero indicates no autocorrelation. Moran's *I* coefficient of the residuals from regression models of the average (a – d), species-specific (e – h) and phylogenetic (i – l) components of colour lightness and body volume with annual mean temperature and annual precipitation respectively.

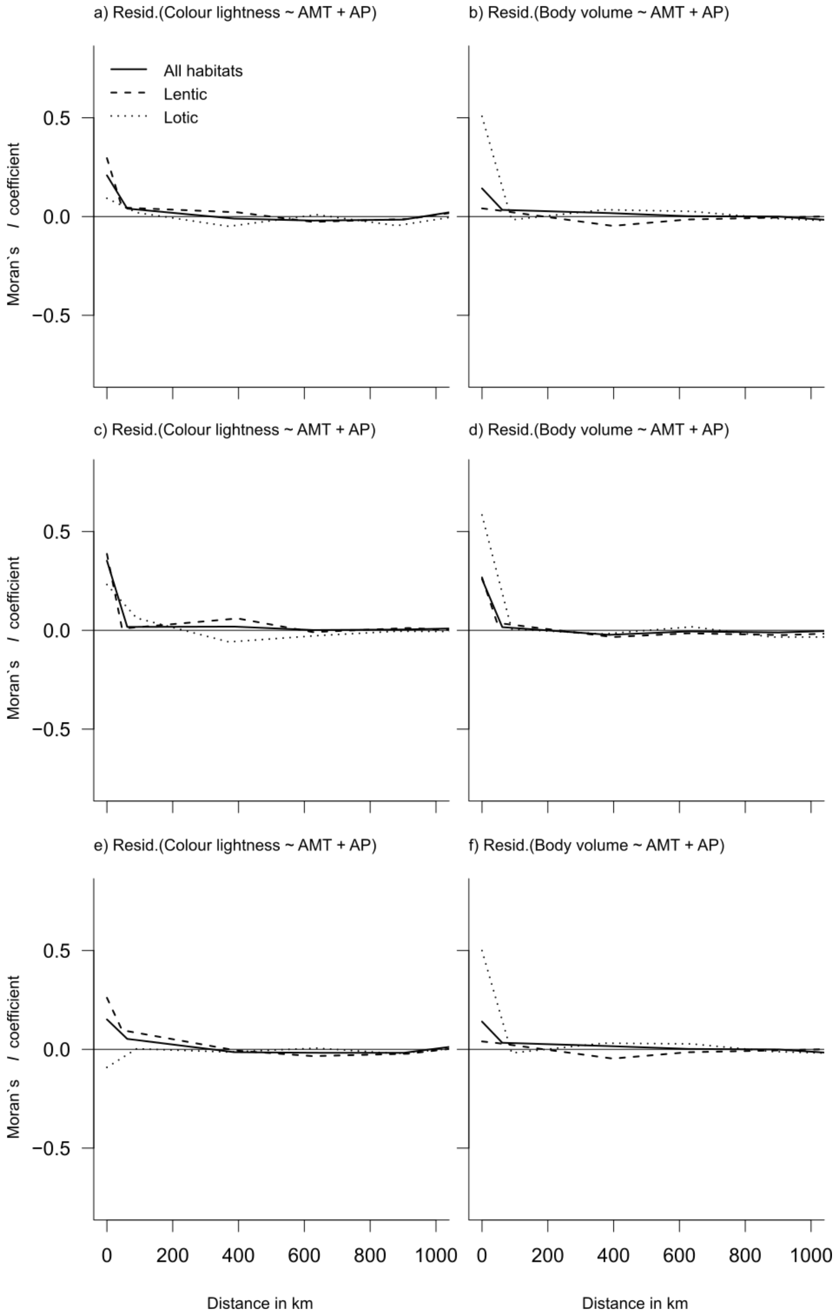

FIGURE S2.2 | Spatial correlogram of Moran's *I* coefficient of the residuals from the multiple regression model of the average, species-specific and phylogenetic components of the average colour lightness and body volume of assemblages of European odonates (all habitats = 518, lentic = 337, lotic = 181) with z-standardized temperature and precipitation variables. The abscissa is distance classes of assemblages and the ordinate Moran's *I* coefficients where a value of zero indicates no autocorrelation. Moran's *I* coefficient of the residuals from regression models of the average (a, b), species-specific (c, d) and the phylogenetic (e, f) component of colour lightness and body volume with annual mean temperature and annual precipitation.

Appendix 2

EXTRINSIC ENVIRONMENTAL FACTORS MODULATE THE RELATIONSHIP BETWEEN INTRINSIC FUNCTIONAL TRAITS AND THE EXTINCTION RISK OF EUROPEAN AND AFRICAN ODONATA

Daniel Acquah-Lamptey, Laura Maehn, Roland Brandl**,** Stefan Pinkert

Manuscript in preparation

Supporting information for Manuscript 3.1

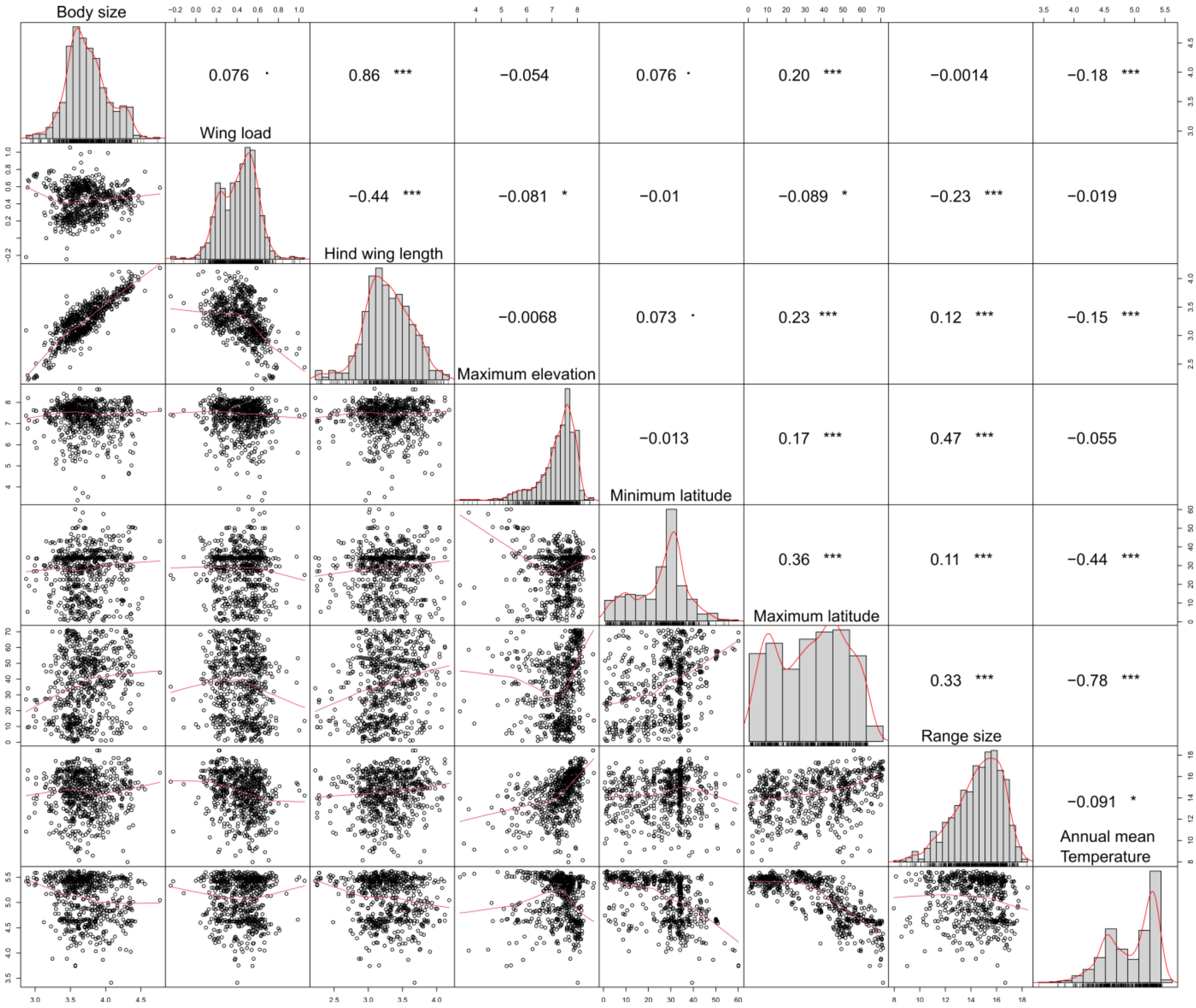

Figure S3.1 | Pair-wise correlation plot matrix between tested variables. Upper panel: Values of Pearson correlation coefficient between trait pairs and the significance level [p-values are indicated as; (***) = 0.001, (**) = 0.01, (*) = 0.05, (.) = 0.1, ( ) = > 0.1]. Diagonal: histogram indicating the frequency distribution of the transformed variables. Lower panel: scatterplots with spline-based smoothed regression lines of each trait pair.

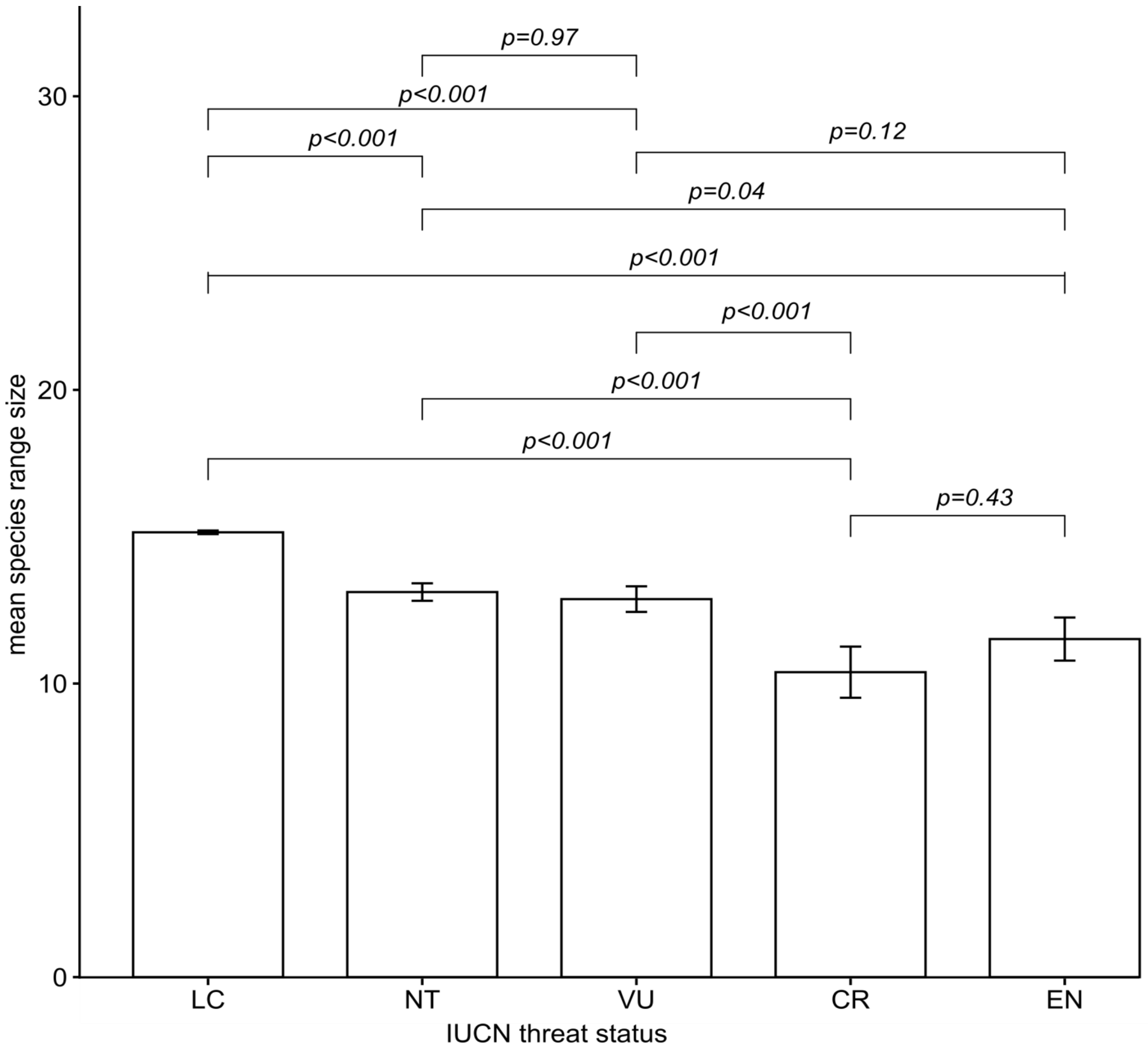

Figure S3.2 | Average range size of African and European odonates in five IUCN threat categories (conservation status). Post-hoc pair-wise comparisons were done using Tukey LSD. LC - least concern, NT - near threatened, VU - vulnerable, CR – critically endangered, and EN – endangered.

TABLE S3.1 | Variance inflation factors of predictor variables from multiple regression models (Table 3.1) that do not account (No) and models that account for the phylogenetic relationship of species (Phy).

Predictors	Vif (No)	Vif (Phy)
Body length	1.09	1.07
Wing load	1.09	1.09
Maximum elevation	1.35	1.38
Minimum latitude	1.18	1.18
Maximum latitude	2.60	3.26
Range size	1.47	1.56
Annual mean temperature	2.52	3.11

Table S3.2 | Individual slopes and standard error (SE) of the predictor variables from linear mixed effect regressions (lme) of the conservation status of European and African dragonfly and damselfly with intrinsic traits and extrinsic environmental variables. Slopes that are significant from zero ($p < 0.05$) are shown in bold. Higher values habitat preference refers to lentic habitats and lower values – lotic habitats. Higher values for continent refer to the European continent while lower values refer to the African continent.

		Single			*Multiple*					
	Traits	Slope ± SE	*t*-value	r^2	Slope ± SE	*t*-value	R^2	Slope ± SE	*t*-value	R^2
Intrinsic	Hind wing length	$7.4 \times 10^{-2} \pm 1.7 \times 10^{-1}$	0.43	0.001						
	Wing load	$-3.5 \times 10^{-2} \pm 3.0 \times 10^{-1}$	–0.12	<0.001	$5.2 \times 10^{-2} \pm 2.8 \times 10^{-1}$	0.19		$8.6 \times 10^{-4} \pm 1.1 \times 10^{-1}$	0.01	
	Habitat preference	**$-3.0 \times 10^{-1} \pm 9.3 \times 10^{-2}$**	–3.23	0.026	**$-2.9 \times 10^{-1} \pm 9.5 \times 10^{-2}$**	–3.04		**$-3.9 \times 10^{-1} \pm 2.0 \times 10^{-1}$**	–1.97	
	Body length	5.5×10^{-2} 1.8×10^{-1}	0.31	<0.001	$6.3 \times 10^{-2} \pm 1.6 \times 10^{-1}$	0.38	0.030	$2.1 \times 10^{-2} \pm 7.2 \times 10^{-2}$	0.3	
Extrinsic	Range size	**$-2.7 \times 10^{-1} \pm 1.6 \times 10^{-2}$**	–16.92	0.347	**$-2.9 \times 10^{-1} \pm 1.8 \times 10^{-2}$**	–16.08		**$-2.6 \times 10^{-1} \pm 2.0 \times 10^{-2}$**	–12.89	
	Continent	**$2.3 \times 10^{-1} \pm 8.3 \times 10^{-2}$**	2.77	0.014	**$3.2 \times 10^{-1} \pm 7.2 \times 10^{-2}$**	4.40		**$3.6 \times 10^{-1} \pm 6.8 \times 10^{-2}$**	5.29	
	Maximum elevation	**$-2.4 \times 10^{-1} \pm 4.2 \times 10^{-2}$**	–5.76	0.047	$2.8 \times 10^{-2} \pm 4.0 \times 10^{-2}$	0.70		$-4.4 \times 10^{-2} \pm 4.2 \times 10^{-2}$	–1.04	
	Maximum latitude	$-3.4 \times 10^{-3} \pm 2.0 \times 10^{-3}$	–1.68	0.007	**$5.2 \times 10^{-3} \pm 2.4 \times 10^{-3}$**	2.16		$3.2 \times 10^{-3} \pm 2.4 \times 10^{-3}$	1.34	
	Minimum latitude	$1.3 \times 10^{-3} \pm 2.7 \times 10^{-3}$	0.48	<0.001	$4.5 \times 10^{-3} \pm 2.4 \times 10^{-3}$	1.89		$3.5 \times 10^{-3} \pm 2.3 \times 10^{-3}$	1.54	
	Annual mean temperature	$5.1 \times 10^{-3} \pm 9.4 \times 10^{-2}$	–0.05	<0.001	**$2.9 \times 10^{-1} \pm 1.1 \times 10^{-1}$**	2.66	0.390	**$2.4 \times 10^{-1} \pm 1.1 \times 10^{-1}$**	2.30	0.386

Table S3.3 | Summary of incomplete and complete Piecewise structural ecological models based on different fits accounting for and without the phylogenetic relationship between species. Final complete model indicated by an asterisk. Significant standardised estimates ($p < 0.05$) are in bold text. Higher values habitat preference refers to lentic habitats and lower values.

		Wing load	Body size	Habitat preference	AMT	Maximum latitude	Range size	Extinction risk
Complete LME model (accounting for phylogenetic relationship). Fischer's C = 13.141, *P*-value = 0.359, df = 12, AIC = 91.141, BIC = 354.643	Wing load		**0.4267**	0.0331		–**0.1344**	–**0.1456**	
	Body size	**0.4267**			0.0192	**0.1605**		
	Habitat preference	0.0331					**0.3182**	0.0245
	AMT		0.0192			–**0.6688**	**0.3430**	0.1007
	Maximum latitude	–**0.1344**	**0.1605**		–**0.6688**		**0.5147**	**0.1591**
	Range size	–**0.1456**		**0.3182**	**0.3430**	**0.5147**		–**0.6429**
	Extinction risk			0.0245	0.1007	**0.1591**	–**0.6429**	
Complete OLS model (not accounting for phylogenetic relationship). Fisher's C = 9.872, *P*-value = 0.452, df = 10, AIC= 59.872, BIC = 164.681	Wing load		0.0620	–**0.1154**		–**0.0948**	–**0.1715**	
	Body size	0.0620			–**0.1522**	**0.1026**	**0.3890**	
	Habitat preference	–**0.1154**				**0.0752**	**0.3532**	0.0422
	AMT		–**0.1522**			–**0.7782**		**0.1573**
	Maximum latitude	–**0.0948**	**0.1026**	**0.0752**	–**0.7782**		**0.4958**	**0.2719**
	Range size	–**0.1715**	**0.3890**	**0.3532**		**0.4958**		–**0.6454**
	Extinction risk			0.0422	**0.1573**	**0.2719**	–**0.6454**	
Complete GLM model (accounting for phylogenetic relationships). Fisher's C = 16.883, *P-value* = 0.154, df = 12, AIC = 74.883, BIC = 196.462	Wing load		**0.4856**	–0.0005		–**0.0865**	–**0.1763**	
	Body size	**0.4856**			–**0.0509**	0.1041		
	Habitat preference	–0.0005						
	AMT		–**0.0509**			–**0.6648**	**0.3517**	**0.1007**
	Maximum latitude	–**0.0865**	**0.1041**		–**0.6648**		**0.5202**	**0.1591**
	Range size	–**0.1763**		**0.3400**	**0.3517**	**0.5202**		–**0.6429**
	Extinction risk			0.0245	**0.1007**	**0.1591**	–**0.6429**	

MT – Annual mean temperature (median), AIC – Akaike information criterion, BIC – Bayesian information criterion, df- Degree of freedom.

Table S3.4 | Summary of incomplete piecewise structural ecological model based on a linear mixed effect model fit accounting for the phylogenetic relationship between species. Fisher's C = 302.838, *P*-value = 0, df = 126. Significant estimates are in bold text. Higher values habitat preference refers to lentic habitats and lower values.

Response	Predictor	Estimate	SE	df	*t*-value	*P*-value	Standard Estimate
Wing load	Habitat preference	–0.0002	0.0157	473.4242	0.0002	0.9891	–0.0005
Wing load	Body size	**0.2646**	0.0316	410.5900	69.2098	< 0.001	0.4856
AMT	Body size	–0.0714	0.0855	342.7945	0.6880	0.4074	–0.0509
Maximum latitude	Body size	**6.6207**	2.6134	169.7736	6.3310	0.0128	0.1041
Maximum latitude	Wing load	–**10.0910**	4.0906	334.2570	5.9996	0.0148	–0.0865
Maximum latitude	AMT	–**30.1066**	1.5029	391.6401	395.9423	< 0.0010	–0.6648
Range size	Habitat preference	**1.3786**	0.1838	343.5323	55.3843	< 0.0010	0.3400
Range size	Wing load	–**1.7580**	0.4810	297.4779	13.1459	0.0003	–0.1763
Range size	AMT	**1.3610**	0.2590	464.7039	27.3295	< 0.0010	0.3517
Range size	Maximum latitude	**0.0444**	0.0058	469.0831	58.8709	< 0.0010	0.5202
Extinction risk	Habitat preference	0.0406	0.0747	285.5016	0.2900	0.5907	0.0245
Extinction risk	Range size	–**0.2629**	0.0181	470.2135	208.8571	< 0.0010	–0.6429
Extinction risk	Maximum latitude	**0.0056**	0.0024	410.1835	5.1950	0.0232	0.1591
Extinction risk	AMT	**0.1593**	0.1057	418.6842	2.2413	0.1351	0.1007

AMT – Annual mean temperature, SE – Standard error, df – degree of freedom.

Appendix 3

EFFECT OF A DRAGONFLY (*BRADINOPYGA STRACHANI* KIRBY, 1900) ON THE DENSITY OF MOSQUITO LARVAE IN A FIELD EXPERIMENT USING MESOCOSMS

Daniel Acquah-Lamptey, Roland Brandl

Supporting information for Manuscript 4.1

Table S4.1 | Model equations using the formalism of R (R Development Core Team, 2016).

Model equations	Probability distribution	Functions and packages used
1: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | count)	Poisson	*glmer* in package *lme4* (Bates et al., 2015)
2a: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | count) +(1 | obs)		
2b: number of larvae ~ container + container : day + shade + (1 | count) + (1 | obs)		
2c: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | obs)		
2d: number of larvae ~ container + container : day + shade + (1 | obs)		
2e: number of larvae ~ container + container : day + shade + (1 | count)		
3: number of larvae ~ container + container : day + shade, random = ~ idh(1 + day) : code + count	-	*MCMCglmm* in package *MCMCglmm* (Hadfield, 2010)
4: number of larvae ~ container + container : day + shade, random = ~ us(1 + day) : code + count		
5: number of larvae ~ container + container : day + shade + (1+day | code) + (1 | count) + (1 | obs)	Negative Binomial	*glmer.nb* in package *lme4*(Bates et al., 2015)

The factor *container* has two levels (open and closed), the factor *shade* also has two levels (shaded and sunlit), *day* is a continuous variables and measures the time since the start of experiment(thereby also an indirect variable for the age of larvae), *count* refers to repeated counts of mosquito larvae, *obs* refers to the observations of each individual container, *code* refers to the codes given to each experimental container, (*1* | *count*) indicates a random intercept of the repeated counts, (*1* | *obs*) the random intercept for each observation, and (*1* + *day* | *code*) a random slope for each container.

Table S4.2 | Summary of model estimates.

	Model 1	Model 2a	Model 2b	Model 2c	Model 2d	Model 2e	Model 3	Model 4	Model 5
Intercept ± Std Error	–0.01 ± 0.80	–0.40 ± 0.76	–0.34 ± 0.15	–0.43 ± 0.75	–0.34 ± 0.15	0.63 ± 0.07	–0.85 ± 0.74	–0.41 ± 0.99	–0.38 ± 0.77
P Value/ PMCMC	0.99	0.59	0.03	0.57	0.03	0.00	0.21	0.64	0.62
Open Containers ± Std Error	–2.71 ± 0.97	–2.67 ± 0.90	–1.61 ± 0.15	–2.59 ± 0.88	–1.61 ± 0.15	–0.99 ± 0.05	–2.19 ± 0.75	–3.09 ± 1.15	–2.71 ± 0.92
P Value/ PMCMC	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Shade ± Std Error	0.96 ± 0.27	0.75 ± 0.42	0.53 ± 0.13	0.76 ± 0.42	0.53 ± 0.13	0.34 ± 0.05	1.45 ± 0.56	0.79 ± 0.45	0.71 ± 0.41
P Value/ PMCMC	0.00	0.07	0.00	0.07	0.00	0.00	0.01	0.08	0.08
Open Container : day ± Std Error	–1.33 ± 0.40	–1.22 ± 0.42	–0.36 ± 0.08	–1.16 ± 0.41	–0.36 ± 0.08	–0.32 ± 0.04	–0.63 ± 0.31	–1.46 ± 0.51	–1.25 ± 0.43
P Value/ PMCMC	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
AIC /DIC	4099.70	3348.10	3585.60	3346.50	3583.60	5261.00	2741.60	2730.80	3349.80

Where applicable, values ± standard errors (SE) are given. To test the robustness of the estimates of model 2d, we modified the model equation by varying the random variables (see Table S4.1). *P* value for Markov Chain Monte Carlo analysis (PMCMC), Akaike information criterion (AIC) and Deviance information criterion (DIC).

S4.3 | Model selection table using the model.sel function in the MuMIn package (Models ranked by AICc(x))

Model	Intercept	Container	Shade	Container: day	Random	df	logLik	AICc	delta	weight
2c	+	+	+	+	(1+day | code) + (1 | obs)	7	–1664.3	3346.7	0	0.693
2a	+	+	+	+	(1+day | code) + (1 | count) +(1 | obs)	10	–1664.1	3348.3	1.63	0.307
2d	+	+	+	+	(1 | obs)	6	–1785.8	3583.7	237	0
2b	+	+	+	+	(1 | count) + (1 | obs)	7	–1785.8	3585.7	239.03	0
1	+	+	+	+	(1+day | code) + (1 | count)	9	–2040.8	4099.8	753.12	0
2e	+	+	+	+	(1 | count)	6	–2624.5	5261.1	1914.43	0

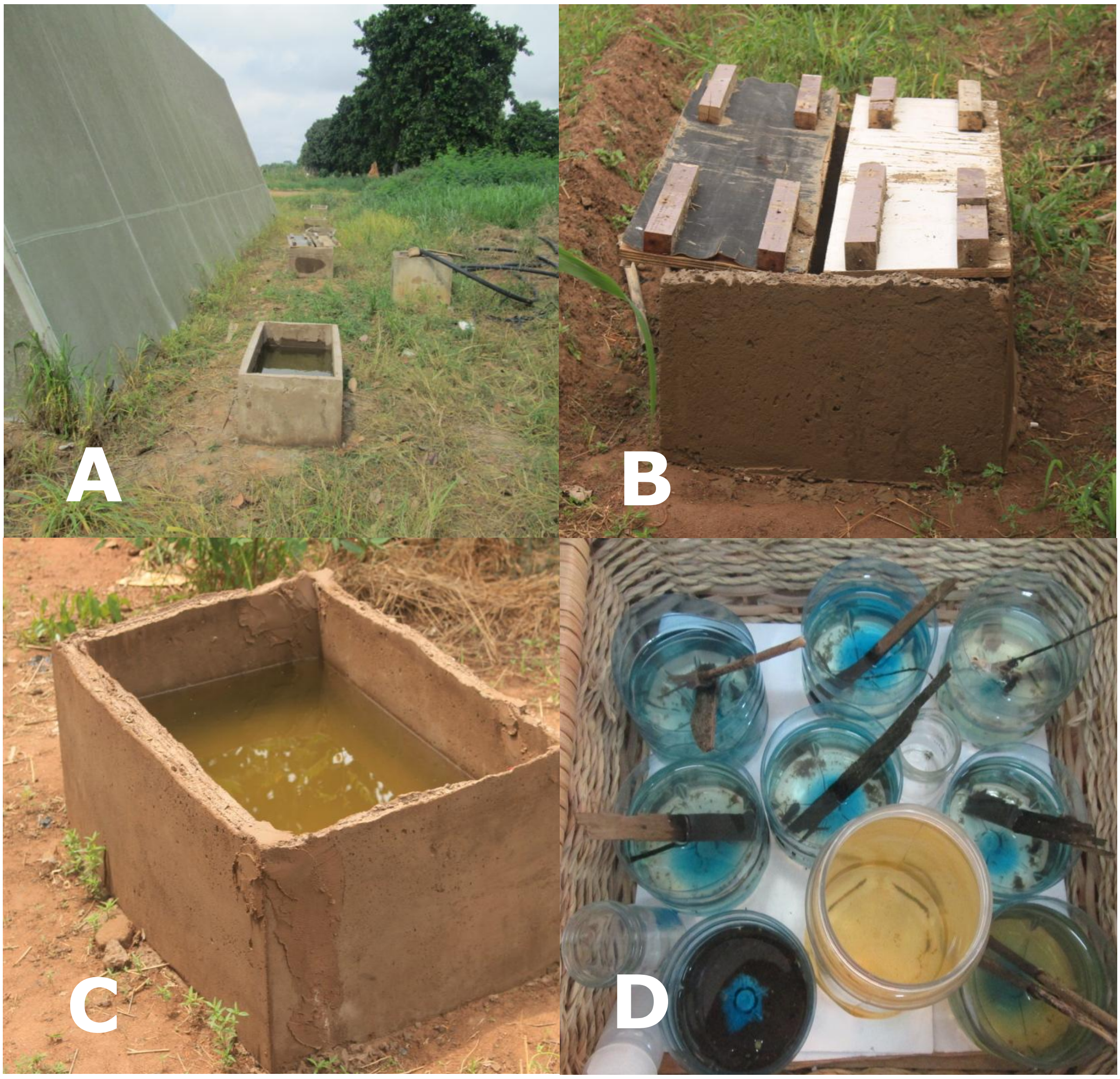

Figure S4.1 | Water storage containers used for our field experiment (A, B, C) and the plastic containers in which odonate larvae transported to laboratory were reared (D). Concrete containers placed directly under the sun (A), closed container (B), open container (C).

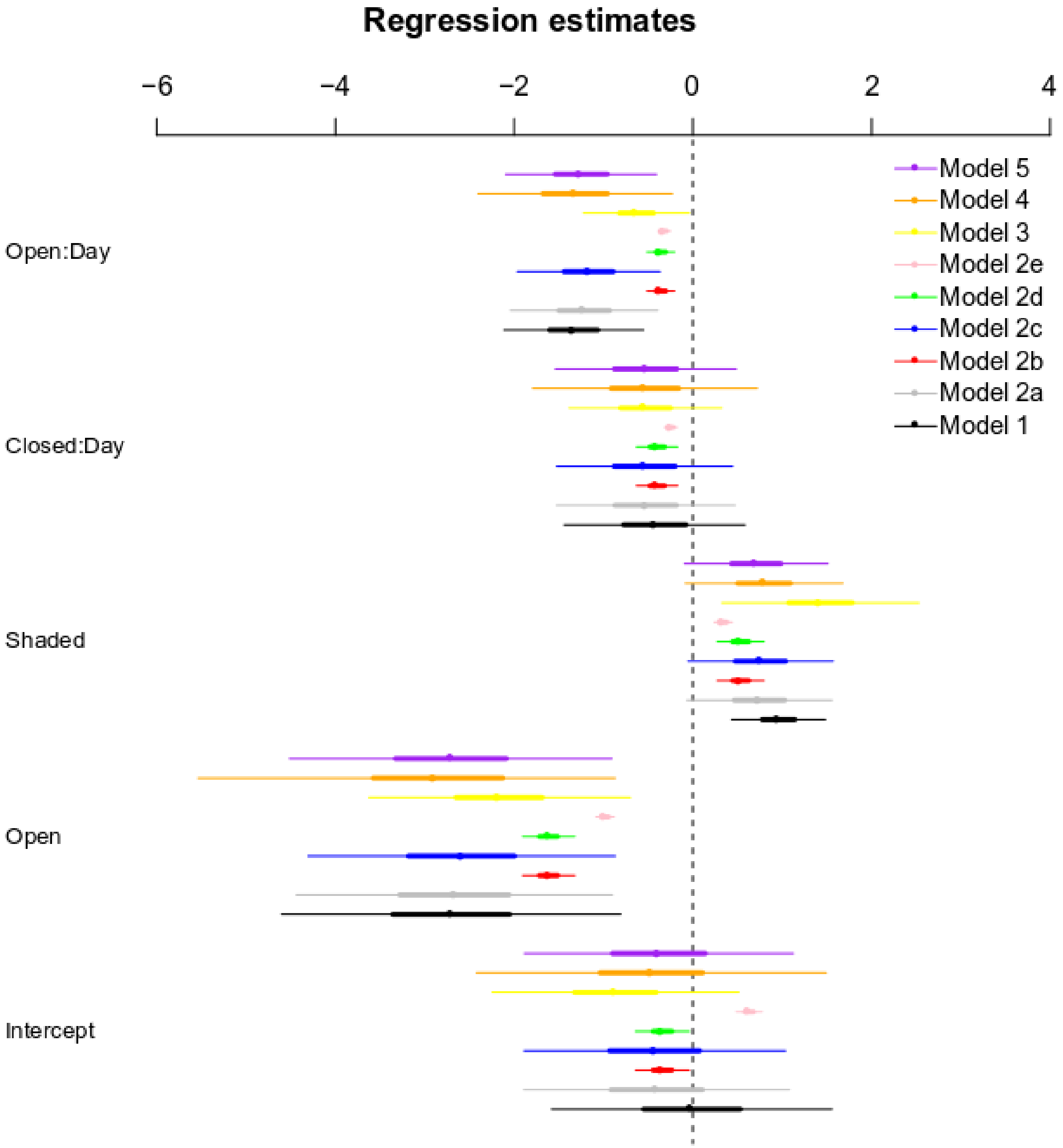

Figure S4.2 | Comparison of the regression estimates of all models. Intercept and factors are shown on the vertical axes. To estimate the impact of the *shade*, container type and time since start of the experiment on the counts of mosquito larvae, we fitted generalized mixed effects models using Poisson distributions (models 1–4) as well as a model using a negative binomial distribution (model 5; Table S4.1). Models 1–2e and 5 used a maximum-likelihood approach, whereas models 3 and 4 used a Bayesian approach (Table S4.1). The figure compares the coefficients, confidence interval values and standard error of the estimated effects (see also Table S4.2).

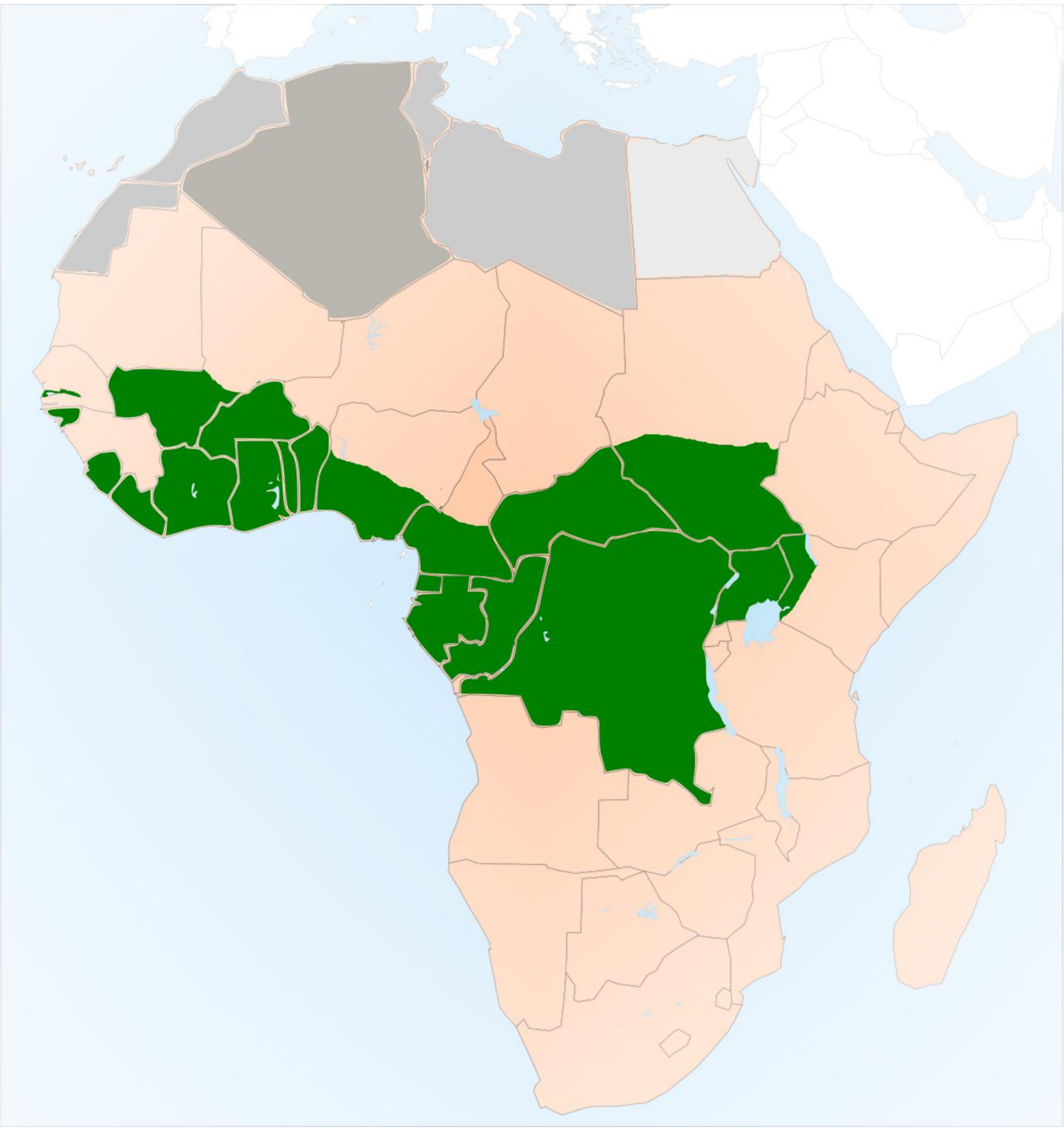

Figure S4.3 | Overlap between the occurrence of malaria and the distributional range of *Bradinopyga strachani* across Africa. The distribution of *B. strachani* has been indicated in green (sourced from Clausnitzer and Dijkstra, 2016). Countries indicated by different shades of grey are either malaria-free or in the phase of eliminating this disease. The distribution of malaria was extracted from World Health Organization (2014).

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OTHER MANUSCRIPTS

- Odonata as focal taxa for biological responses to climate change
- Awareness of odonata (dragonflies and damselflies), an important insect order, among graduates in the Greater Accra region of Ghana
- Butterfly Diversity: An Indicator for Environmental Health within Tarkwa Gold Mine, Ghana.
- Using Orthoptera and Hymenoptera indicator groups as evidence of degradation in a mining concession (Tarkwa gold mine) in Ghana.
- Butterfly Assemblages of Two Wetlands: Response of Biodiversity to Different Environmental Stressors in Sierra Leone.

ODONATA AS FOCAL TAXA FOR BIOLOGICAL RESPONSES TO CLIMATE CHANGE

Stefan Pinkert, Viola Clausnitzer, **Daniel Acquah-Lamptey**, Paulo De Marco, Frank Johansson (2022).

In Córdoba-Aguilar, A., Beatty, C., Bried, J. T., and Suárez-Tovar C. M. (eds.). *Dragonflies & Damselflies: Model Organisms for Ecological and Evolutionary Research*, 2nd edition. Oxford Academic. https://doi.org/10.1093/oso/9780192898623.003.0027

ABSTRACT

Adaptations to novel climates have been a motor for the evolution of life on Earth, but the human-caused rise of global temperatures is unprecedented in its velocity and many species may not be able to cope with such rapid climatic changes. The most likely scenarios indicate that, until the end of this century, the increase of global temperatures above the pre-industrial levels will be of comparable magnitude as changes since the last glacial maximum (LGM). Species that cannot adapt fast enough to these dramatic changes have to shift their distributions or phenology, or they become locally extinct. How species react depends on a multitude of intrinsic factors, including life history traits, physiological adaptations, and dispersal ability. This chapter first explains why Odonata are an ideal taxon to understand and globally monitor biological responses of both aquatic and terrestrial insects. In addition, it provides an overview of important environmental drivers of contemporary diversity patterns of Odonata. Finally, it reviews literature on range shifts, population trends, and phenological changes in Odonata and discusses the importance of functional traits—not only for predicting how, but also for understanding why, species respond to climatic changes.

AWARENESS OF ODONATA (DRAGONFLIES AND DAMSELFLIES), AN IMPORTANT INSECT ORDER, AMONG GRADUATES IN THE GREATER ACCRA REGION OF GHANA

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Manuscript in preparation

ABSTRACT

Odonata (dragonflies and damselflies) represent one of the most popular insect groups. They are good indicators of aquatic ecosystem health and can serve as biological control agents of pests including mosquitoes. Using questionnaires, we examine the perceptions and awareness of Ghanaian graduates and solicited knowledge on Odonates, their ecology, and conservation. We then assessed the knowledge of the respondents on the state of water bodies and forests. Respondents had knowledge of Odonates and provided vernacular names which were not species-specific. These names showed inherent connections to their conservation, behavior, and ecology. Respondents perceived Odonates to be beneficial and related to forests and water bodies. Respondents show high level of knowledge of the importance of and threats facing water bodies and forests in the country. The awareness and local knowledge of Odonates is vital for promoting insect biodiversity in general and encouraging local community support in their conservation and application in biological control.

INTRODUCTION

Odonata (dragonflies and damselflies) represent one of the historically most studied and first insect groups to be assessed on a global scale (Clausnitzer et al., 2009; Pinkert et al., 2020). Odonates are good bioindicators of environmental health. As freshwater insects, dragonflies and damselflies are exceptionally vulnerable to human activities such as pollution of freshwater systems, urban and agricultural expansion, and forest cover loss affecting water sources). The sensitivity of Odonates to habitat structure such as forest cover and habitat quality such as water clarity (Stewart & Samways, 1998; Sahlén, 1999) makes them useful for the selection of new areas for protection (Simaika and Samways, 2009; Clausnitzer et al., 2017) and the identification of important landscape characteristics (Raebel et al., 2012). Therefore Odonates have been recommended as one of the much easier bio-tools for the monitoring and evaluation of habitat quality (Smith et al., 2007; Lunde and Resh, 2012). As biological control agents, Acquah-Lamptey and Brandl (2018) showed that the presence of the dragonfly, *Bradinopyga strachani*, in water storage containers (used predominantly among rural Ghanaians and those in the construction industry) significantly reduced the density of mosquito larvae. Despite this promising mosquito control strategy, Sebastian et al. (1990), in a successful study conducted in Southeast Asia, among other things, attributed the awareness and enthusiastic participation of local households to the success of the control strategy. Odonata research in Ghana began more than a century ago without any Ghanaian Odonata enthusiast. The most remarkable study is Djikstra (2007), who compiled the first comprehensive national inventory of 177 species. Over the past decade, a number of Ghanaian ecologists have been working on environmental monitoring (Acquah-Lamptey et al., 2013a; Kyerematen et al., 2014a, 2014b; Seidu et al., 2017, 2018, 2019), and biological control (Acquah-Lamptey and Brandl, 2018). Ghana is estimated to home about 226 Odonates with highly range-restricted and rare species occurring within forests (Dijkstra and Clausnitzer, 2006).

Despite the copious contributions of local knowledge to biodiversity conservation (Colding and Folke, 2001), there are concerns that with development, urbanization, and modernization, local knowledge systems, together with their channels of propagation, could be lost. This is because the traditional beliefs that upheld indigenous conservation of natural resources like forests, rivers, and their associated fauna are becoming weaker (Ntiamoa-Baidu, 2008; Kothari, 2007). The Aichi Biodiversity Targets 1 and 18 highlight the awareness of the values of biodiversity, and the importance of traditional knowledge and practices of indigenous and local communities to biodiversity conservation (CBD Secretariat, 2010). As a signatory, Ghana adopted a National Biodiversity Strategy and Action Plan (NBSAP) aiming to document traditional knowledge, integrate it with formal science in biodiversity conservation, and promote public awareness, appreciation, and support for biodiversity conservation (MESTI, 2015).

In Ghana, some animals including threatened species are regarded as totems due to their historical and socio-cultural significance to the indigenes (Attuquayefio and Fobil, 2005). Similarly, some trees as well as forest patches are left protected because of the belief that they host ancestral or divine spirits (Abayie Boaten, 1998). The research on local knowledge systems relating to biodiversity have focused on the conservation of biophysical environments (e.g., Ayaa and Waswa, 2016), traditional wildlife and spiritually related knowledge (e.g. Bortolamiol et al., 2018), native beekeeping (e.g., Park and Youn, 2012), ethnobotanical approaches (e.g. Pei et al., 2009), contribution to forest conservation and management (e.g., Boafo et al., 2015; Camacho et al., 2016; Osei-Tutu, 2017). However, studies on local knowledge of insects focused on their importance; as food (e.g., Anankware et al., 2016; Kagezi et al., 2010a), their by-products (e.g., Karikari and Kwapong, 2007), and in pest management (e.g., Kagezi et al., 2010b; Akutse et al., 2011; Maayiem et al., 2012).

In this study, we investigate the perception of some Ghanaian graduates on dragonflies and damselflies, local knowledge of the species, and their perceived importance. We also assess the awareness of the respondents on the state of water bodies and forests in Ghana. We predict that the knowledge of Ghanaians of dragonflies and damselflies could be embedded in their naming. Similarly, Ghanaians should be aware of the state of forests and water bodies as the culture of Ghanaians to a large extent revolves around their biophysical environment. This study to a large extend becomes the first of its kind to assess local knowledge of invertebrates in the country.

MATERIALS AND METHODS

Study area

The Greater Accra region is the smallest of Ghana’s 16 regions and forms about 1.4 percent of the total land area. It is the second most populated region with an estimated population of about 5 million (Ghana Statistical Service, 2020). The region is located in the southern part of country and shares borders with the Central region (West), Eastern region (North), Volta region (East) and the Gulf of Guinea (south). The Greater Accra is the most urbanized region in Ghana with over 90 % of its population living in urban centres (Ghana Statistical Service, 2014). The high population and density of the region is said to be driven by a high population growth rate and in-migration from other regions and the rural hinterlands. The in-migration into the region is highly motivated by the fact that the region holds the seat of Government, administrative, communications and economic centre as well as hosts the most tertiary institutions in the country. These in-migrations have contributed to the region being the most ethnically diverse in Ghana with 39.7 % Akans, 27.4 % Ga-Dangmes, 20.1 % Ewes, 5.2 % Mole-Dagbons, and 7.6 % other minor ethnic groups (Ghana Statistical Service, 2012). As the population density of the region increases, land use and land cover increases resulting in a decrease in vegetation cover. While the national forest coverage reduced by 20 % between the year 2000 and 2013, the Greater Accra region lost 10 % in vegetation cover between 2002 and 2010 (Stow et al., 2013). The main rivers flowing through the region are the Densu and Volta as well as some seasonal streams flowing through many lagoons into the Gulf of Guinea. With the increasing population and infrastructural development, Accra is also characterized by the development of settlements along major river banks (Karley, 2009).

Data collection

Ghanaian participants in the Greater Accra region were randomly recruited through online invitations to respond to a set of structured open- and close-ended questions between September 2019 and April 2020. Others were interviewed based on the questionnaire and responses transmitted into the online database on their behalf. The online questionnaire was generated using SoSci Survey (Leiner, 2019) and was made available to users via www.soscisurvey.de. In total 166 participants responded to the questionnaire. The questionnaire sought to assess their awareness of dragonflies and damselflies, some aspects of Odonate biology such as the identification of and differences between dragonflies and damselflies, importance or benefits derived from the insects, as well as knowledge of the association of dragonflies and damselflies to water bodies and forests. Using standard pictures of common insects, respondents were asked to identify dragonflies and damselflies. Respondents provided vernacular names of dragonflies and damselflies. The vernacular names provided were then validated by follow up contacts to respondents as the survey allowed access to personal details of respondents and also by selected professionals in the various languages. As far as possible the meaning and significant of each name was traced. The questionnaire assessed the respondents' awareness of some natural resources (rivers and forests) in their surroundings and their perceived importance and threats facing these natural resources.

Data analysis

Survey data were downloaded, processed, and analyzed. Summaries of responses were presented as bar and box plots. We analyzed the relationship between counts of response variables as surrogates of awareness as the dependent variable and gender, region of origin, educational level, and age group of the respondents as the independent variables using generalized linear models with a Poisson error and a log-link function. Analyses were done using R statistical package (R Development Core Team, 2020).

Demographic profile of the respondents

Males made up majority of the respondents who completed the survey. All the respondents were within the 18-64 year age range with the majority (66.9%) belonging to the 25-34 year age group. A majority of eighty-six (53.8 %) have a University bachelor degree. Despite recruiting participants resident in the Greater Accra region, 67 % of the respondents originated from 10 other regions in Ghana (Table 1).

Table 1 | Demographic profile of respondents.

Gender	Frequency	%	Age group	Frequency	%	Educational level	Frequency	%	Region of origin	Frequency	%
Male	96	57.8	18-24	15	9.2	Higher National Diploma	3	1.9	Ashanti	16	9.8
Female	70	42.2	25-34	109	66.9	University Bachelor Degree	86	53.8	Bono	4	2.5
			35-44	35	21.5	University Masters Degree	71	44.4	Central	19	11.7
			45-54	2	1.2				Eastern	24	14.7
			55-64	2	1.2				Greater Accra	54	33.1
									Northern	3	1.87
									Oti	6	3.7
									Upper East	7	4.3
									Volta	23	14.1
									Western North	1	0.6
									Western	6	3.7

% - Percentage of frequency per total number of respondents

RESULTS

Awareness and knowledge of dragonflies and damselflies

The majority of the respondents (95%) had knowledge of dragonflies while 57% knew damselflies (Table 2). Despite claiming to know dragonflies and damselflies, 68% of the respondents identified dragonflies correctly, whiles 61% correctly identified damselflies. When asked about if dragonflies differed from damselflies, only 45% of the respondents replied in the affirmative. This was reflected in the mix up in the identification of a dragonfly image from that of damselfly. Subsequently, respondents irrespective of the prior agreed dragonflies and damselflies varied mostly in their body form, wing shape, and body colouration (Figure 1).

When asked when and where they sighted dragonflies and damselflies, both were reported to be sighted mostly near ponds, rivers, and grass fields on hot sunny days during the rainy season (Figure 1). When quizzed about the diversity of Odonates, the majority of respondents were not sure of the diversity (species richness) (Table 2). This reflected in the majority of the respondents not being aware of the state and change in Odonates abundance over the past 5 years (Table 2). However, the respondents believed Odonata diversity was most threatened by climate change and water pollution (Figure 2). About 72 % of the respondents considered dragonflies and damselflies as important insects. However, the majority of these respondents attributed the importance of Odonates to the importance of biodiversity in general. Respondents perceived Odonates to be useful as biological control agents, food source, and have cultural value (Figure 2). The respondents showed different levels of awareness of Odonates ranging from 2 to 38 (Figure 3). Regression models showed that the surrogates of awareness of the respondents were influenced by their demography (Figure 3, Table 4).

Table 2 | Perception of Ghanaian graduates of dragonflies and damselflies

	Response frequency (percentage)			
	Yes	No	Not sure or Do not know	Interchanged
Knowledge of dragonflies	188 (94.9 %)	10 (5.1 %)		
Knowledge of damselflies	107 (56.6 %)	82 (43.4 %)		
Are they different?	90 (45.3%)	107 (54.7%)		
Dragonfly picture identification	146 (67.9 %)	11 (5.1%)		58 (27.0%)
Damselfly picture identification	132 (61.4%)	58 (27.0%)		25 (11.6%)
Awareness of Odonate diversity	23 (11.9 %)	7 (3.6 %)	163 (84.5 %)	
Relation of Odonates to water	116 (60.7 %)	8 (4.2 %)	67 (35.1 %)	
Relation of Odonates to forest	99 (52.4 %)	13 (6.9 %)	77 (40.7 %)	
Awareness of change in Odonate diversity	79 (41.8 %)		110 (58.2 %)	
Are Odonates important?	128 (71.9 %)	1 (0.6 %)	49 (27.5 %)	

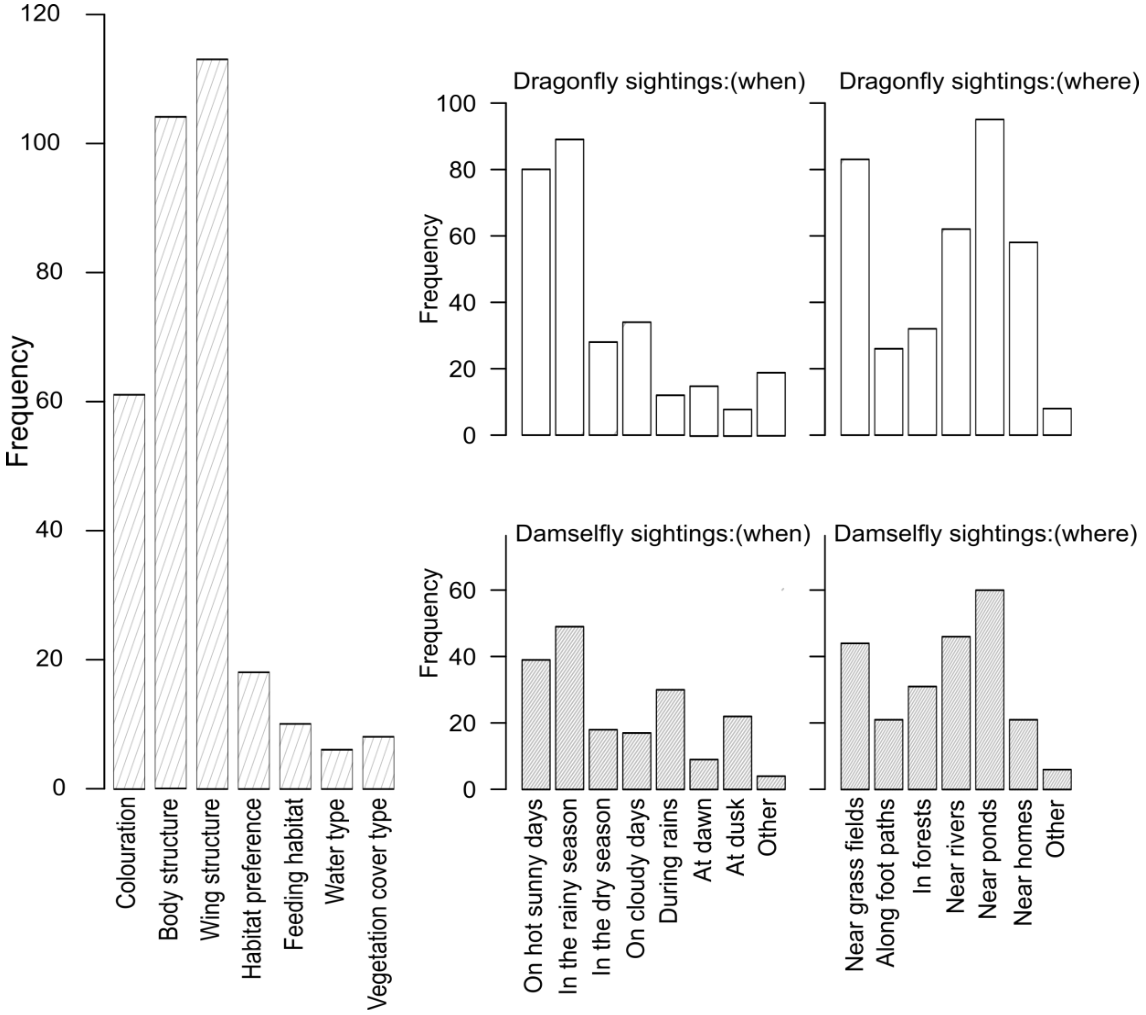

Figure 1 | Respondent's perception on the morphology and ecology of Odonates (Striped bars illustrate - differences between dragonflies and damselflies, shaded bars and open bars represent - when and where damselflies and dragonflies are sighted respectively).

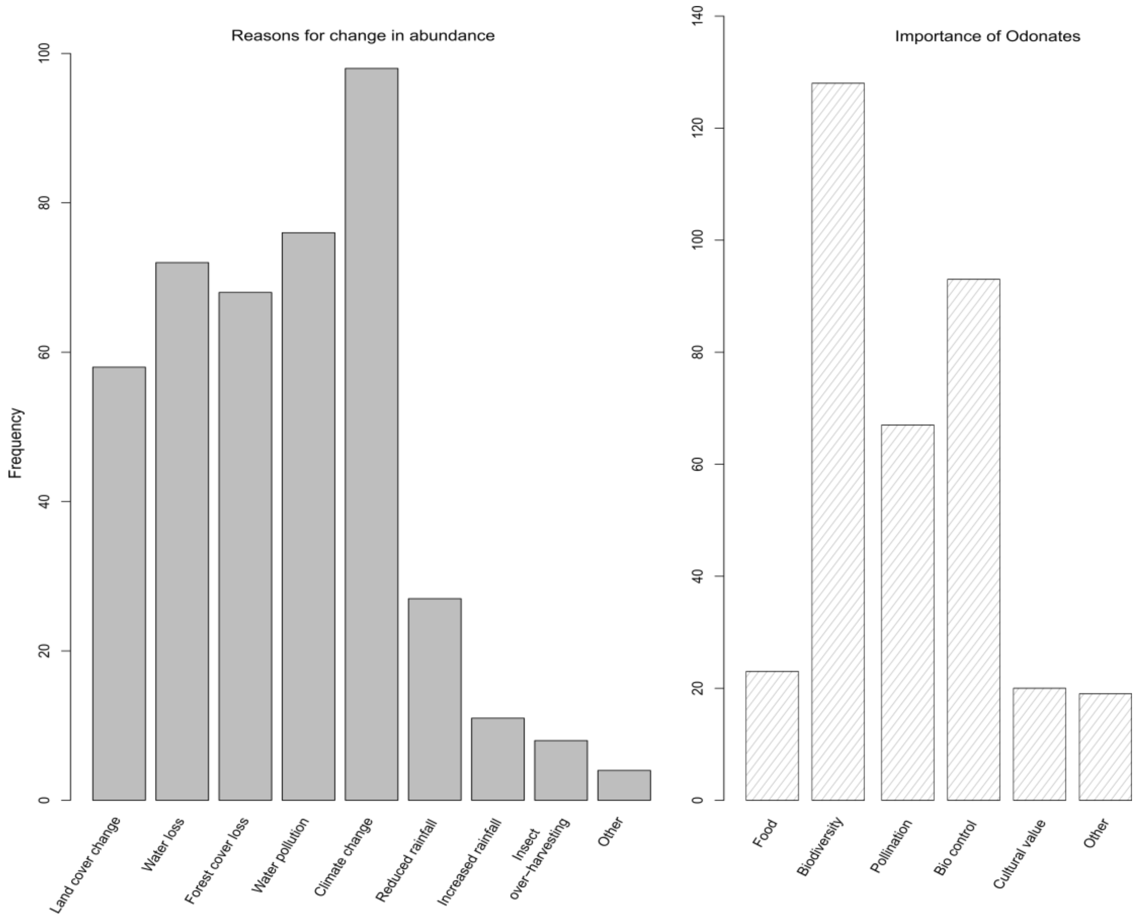

Figure 2 | Respondents' perception on the importance of Odonates (striped bars) and factors affecting Odonate species abundance (grey bars).

Table 3 | Ghanaian vernacular names for dragonflies and damselflies.

Vernacular names	**Languages**	**Literal meaning / explanation**
Saa paga	Dagbani	Wife of rain
Akyankyanka/ kyankyanka	Nchumuru	Dance around
Gbekɛbiia kɔɔyɔɔmli lɛlɛ	Ga	Kids aeroplane
Sɔɔdee/ Ansɔdee	Ga	Reference to the ability to be perched on (mounted). It is further explained that, the clearly visible segmented and elongated abdomen looks like a floor available for perching. *Sɔɔdee* also refers to storeys (e.g. *wɛiŋ tsu sɔɔdee ekpaa* means six storey apartment).
Numliaga	Ga	Water hopper (water grasshopper)
Taadu /Taru	Ewe	Conspicuous shape and size of the head, one is believed to get a headache (used to prevent people from killing the harmless insect).
Atsufui	Ewe	Damselfly - Twin (female) because of tandem pairs
Kawɛtoore	Kasem	Wɛtoore means late afternoon, associating their sightings in the afternoon
Agyegyensu	Fante	Purifies water/ disturbs water stillness
Agyanka	Twi/Fante	Orphan
Nkwadaa Wiemuhyɛn	Twi/ Fante	Kids aeroplane
Atetensu	Twi	Perch along water body and purifies it/ disturbs water stillness
Kwakubonsua/ Bonsuo	Twi	Hitting the water surface - (females dip abdomen in water in flight during egg laying
Atekrede	Twi	†
Ukpembal	Konkomba	†
Dohdomonn	Konkomba	†

† - Unconfirmed names

Local names of dragonflies and damselflies

In assessing the knowledge of dragonflies and damselflies among Ghanaians, participants were asked to identify dragonflies and damselflies in their local Ghanaian languages (Table 3). From seven languages, we compiled and verified 13 vernacular names of Odonates. Though there were no indications of the names being species-specific, they depicted some ecological, morphological, and behavioural characteristics of dragonflies and in an instance, a damselfly.

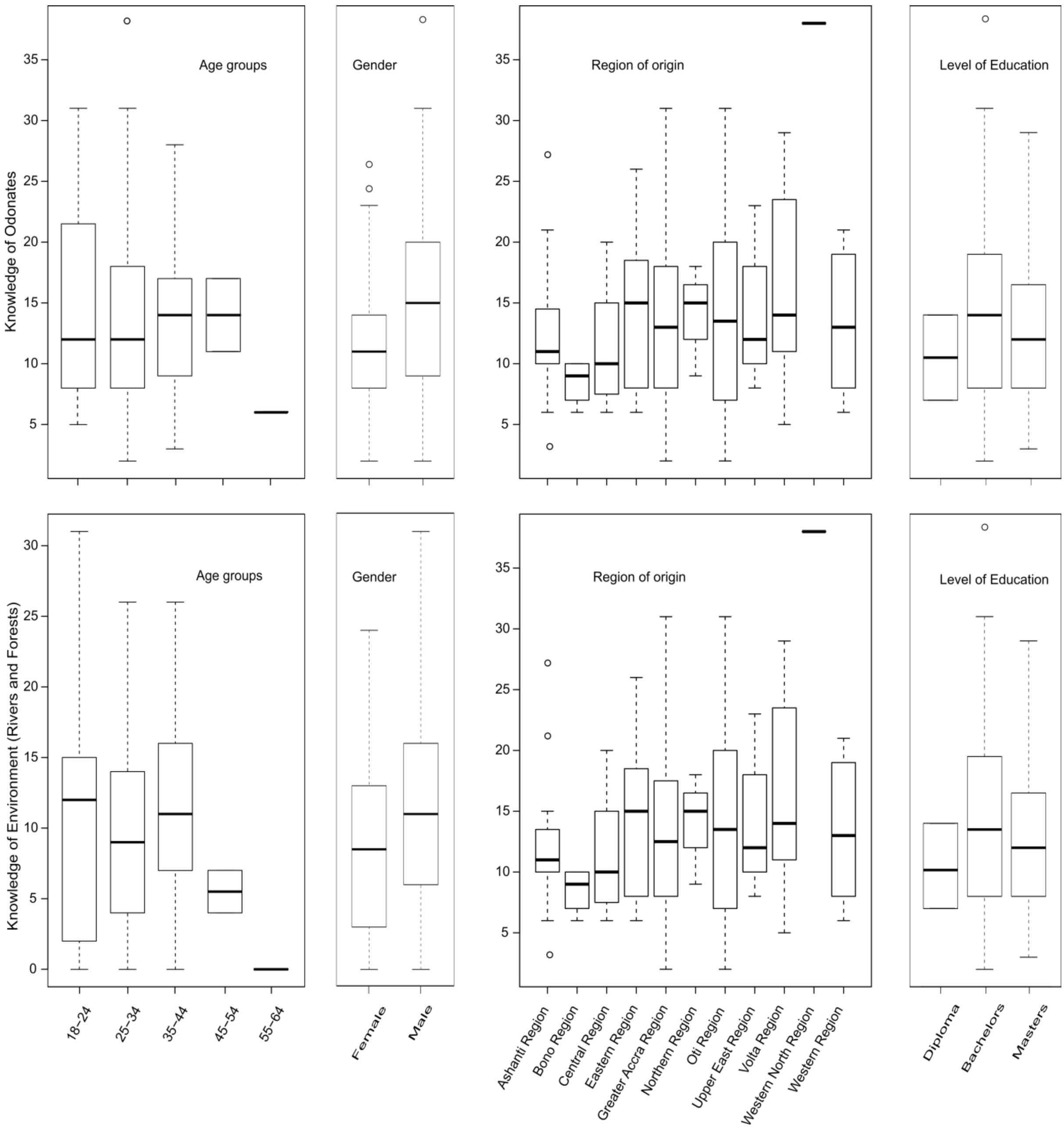

Figure 3 | Demographic distribution of respondents' perception and awareness of Odonates and the environment (Rivers and Forest).

Table 4 | P-values (of type II analyses) of the ordinary least square regression and generalised linear model (error Poisson; log-link function) of the surrogates of awareness (number of responses) of dragonflies and damselflies in relation to respondents' age, education, region of origin and gender.

	Model	Age (*P*)	Education (*P*)	Region (*P*)	Gender (*P*)
Awareness of Odonates (sum of responses)	Least square	0.139	0.106	0.065	**0.004**
	Poisson	0.157	**0.001**	**<0.001**	**<0.001**
Awareness of the Environment (water bodies and forests)	Least square	0.139	0.106	0.259	**0.004**
	Poisson	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Awareness of water bodies and forest conservation

Respondents affirmed that Odonates have a relationship with water bodies and forests (Table 2). Based on that, we sought their level of awareness of the state of surrounding water bodies and forests reserves. Respondents attributed some importance such as fish source, home to other organisms and source of water for domestic and agricultural use to water bodies. They also named some importance of forests including watershed and source of bush meat. In a likewise manner, the respondents showed their level of awareness of threats facing water bodies and forests reserves. These included illegal mining, housing/infrastructural development, and tree cutting/deforestation (Figure 4). Regression models showed evidence that the surrogate for awareness of the respondents on current threats facing and importance of water bodies and forest reserves is dependent on the educational level and gender of the respondents (Table 4).

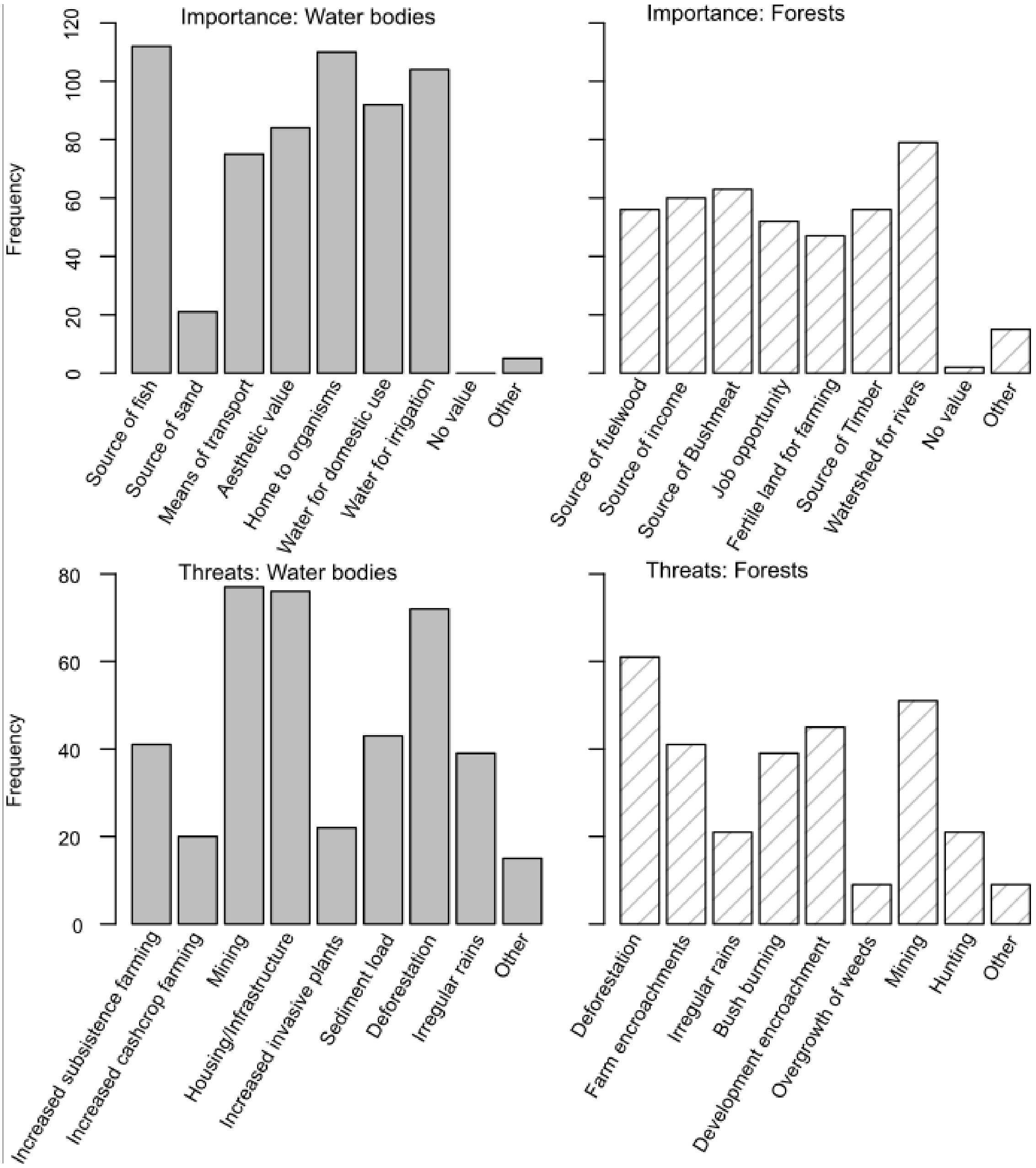

Figure 4 | Respondents' perception of the values (top) and threats (bottom) facing water bodies (shaded bars) and forest reserves (striped bars).

DISCUSSION

Awareness and knowledge of dragonflies and damselflies

Studies on local knowledge of fauna in Ghana are rare with only a few directed towards termites (Maayiem et al., 2012; Akutse et al., 2011), bees (Karikari and Kwapong, 2007) and birds (Deikumah et al., 2015) while some studies have been on entomophagy in Ghana (e.g. Anankware et al., 2015, 2016). Over the past 10 years, there has been a growing interest in Odonata studies in Ghana relating to habitat assessment and monitoring (Acquah-Lamptey et al., 2013a; Seidu et al., 2017, 2018; Kyerematen et al., 2014a, 2014b) and biological control (Acquah-Lamptey and Brandl, 2018). This study is the first Ghanaian-led research on the awareness of Odonates and the assessment of the local knowledge on invertebrates not directly linked with food among Ghanaians.

Our findings showed that, though the respondents know about Odonates, more respondents are aware of dragonflies than damselflies (Table 2) because the former are more conspicuous. Dragonflies can easily be encountered near homes than damselflies which are more restricted to water bodies and forests and hardly occur very far from their breeding grounds. This is corroborated by the fact that there was only an instance where the vernacular name referred specifically to a damselfly (*Atsufui* in Ewe, Table 3). Some respondents could identify Odonates from pictures and agreed they differed in body structure (Figure 1: wing shape, body form, and colouration). Interestingly, the majority of these respondents believed that dragonflies and damselflies are the same insect (Table 2). This is reflected in the naming system where both dragonflies and damselflies are referred to by the same local names (e.g., G*bekɛbiia kɔɔyɔɔmli lɛlɛ*, *Nkwadaa Wiemuhyɛn* etc). A similar case is seen in many African countries where some insect groups are referred to by the same local name (e.g., Münke-Svendsen et al., 2016). Among the T’boli people of the Philippines, both dragonflies and damselflies are called *Klowong* (Cudera et al., 2020). Also, the people of Socotra refer to the dragonfly as ***íˀdbəhur*** meaning ‘armoured flying insect (that stings)’ or, more generally, a ‘flying insect that makes a buzzing noise’ (Van Damme et al., 2020). Another instance is reported by Cockburn et al. (2014) where in isiZulu folk taxonomy, some insects bear names that correspond to a group and not necessarily a species and as such names that refer to an insect species usually occurs when there is a personal connection between the insect and the people.

Odonates can be found anywhere and at anytime, but they are best observed near their breeding habitats (water bodies) and on warm sunny days. The territorial behaviour of males, oviposition of females around water bodies, and thermoregulatory behaviours (basking, wing whirring) increase the chance of them being spotted in certain areas. This corroborated with the respondents’ responses on when and where Odonates were sighted (Figure 1).

After developing a National Biodiversity Strategy and Action Plan (NBSAP) to promote public appreciation and support for biodiversity conservation, Ghana developed a climate change education program to improve the public’s understanding of climate change (Brittlebank, 2015). Before then, there was little climate change education in the national education curriculum (Boakye, 2015; Boateng, 2015). Currently, there is hardly any mention of Odonata at any stage of the Ghanaian academic curriculum except for third-year students in only two Ghanaian universities running Zoology-related courses. The respondents’ low awareness and knowledge of Odonates can be because these important insects are hardly mentioned in any formal academic curriculum and due to the lack of documentation and public awareness campaigns involving insects in general; a probable reason for the insignificant contribution of education to the respondents’ knowledge. The main insects that benefit from such campaigns are those of public health importance such as mosquitoes and houseflies. The respondents’ perception that climate change and water pollution affected Odonata diversity the most (Figure 2) despite a lot not being aware of changes in Odonate diversity (Table 2), can be attributed to the drastic increase in climate science education as evident in the number of new courses taught for instance in the University of Ghana and the increase in public interactions to create awareness on climate change and biodiversity by institutions such as the Centre for Climate Change and Sustainability Studies (C3SS) and the Ghana Wildlife Society (GWS) (Ghana Wildlife Society, 2017, 2018; C3SS, 2019).

To most respondents, all biodiversity is valuable and also attributed cultural value and source of food as some importance of Odonates (Figure 2). Among Ghanaians, several animals are considered totems (Abayie Boaten, 1998) and hence are protected. However, the name *Taadu* in the Ewe language is the first mention of Odonates in the cultural or belief system in Ghana. Entomophagy is a common practice in Sub-Saharan Africa (Van Huis, 2003). Despite making a percentage of consumed insects in Africa (Van Huis et al., 2013), there is no record of dragonflies and damselflies as edible insects in Ghana (see Anankware et al., 2015, 2016). The perceived importance of Odonates is a good foundation to raise awareness of the importance of Odonates and garner support for their use in the biological control of mosquitoes and as flagship species for the conservation of wetlands. The respondents have demonstrated some self-acquired knowledge and awareness of dragonflies and damselflies. We cannot attribute this awareness to national efforts made to promote public awareness, appreciation, and support for biodiversity conservation as per the Convention on Biological Diversity Aichi Targets 1 and 18. However, it is a good foundation for its promotion.

Factors such as age, gender, experiences, ethnicity, occupation, cultural, and religious beliefs influence the acquisition of indigenous knowledge (Ayantunde et al., 2008; Magni, 2016). In many indigenous societies, the roles and responsibilities of males and females vary (Anderson, 2016). The roles and responsibilities of men in the community expose them more to these unknown yet important insect taxa. Males are adventurous and more likely to play with insects than females. As a respondent said; “As children, *we used sticky traps to capture dragonflies to play with. We were fascinated by their appearance, their colouration, their wings, and the sound of the fluttering wings”*. Similarly, females who often visit the riverside to fetch water for household activities are more likely to see Odonates but may be less intrigued to explore them. Odonate diversity and distribution depend on habitat availability, structure, and quality (Sahlén, 1999; Stewart and Samways, 1998; Dijkstra and Clausnitzer, 2006). Therefore the respondents’ place of residence is likely to influence their encounter and awareness of the insects, that is, respondents located in areas with more Odonate habitats are likely to encounter and be more aware of Odonates.

Local names of dragonflies and damselflies

In Ghana, there are Species-specific vernacular names for several birds (Diekumah et al., 2015), some bees (Karikari and Kwapong, 2007), and some edible insects (Anankware et al., 2016) because of their association with humans. The compilation of 13 names from 7 languages is similar to the case of South Africa where there exist multiple names for Odonates including multiple names in a single language (Vick, 1999; Tarboton and Tarboton, 2015).

According to Diekumah et al. (2015), indigenous nomenclature is guided by the species’ morphological characteristics or belief systems of the local people. The vernacular names of dragonflies and damselflies are informed by their morphological characteristics. *Taadu* in the Ewe language emphasizes the prominent shape and size of the head and eyes of damselflies; *Gbekɛbiia kɔɔyɔɔmli lɛlɛ* and *Nkwalaa Wiemuhyɛn* in Ga and Akan languages respectively because of the resemblance of the Odonate body structure to aeroplanes. This is also seen in Cockburn et al. (2014) who report that in isiZulu folk taxonomy, some insect names designate the physical form of the insect. The name *Sɔɔdee* or *Ansɔdee* in the Ga language shows that people are aware of the segmentation of the abdomen of Odonates. The name originated from *Sɔɔdee* which means to floors/levels of high-rise buildings and makes reference to the elongated and segmented abdomen.

The vernacular names of dragonflies and damselflies are also informed by their behaviour. *Bonsuo* (hit water), *Numliaga* (water hopper), and *Atentensu* (disturb the stillness of water) refer to the egg-laying behaviour of the females as they repeatedly dip the tips of the abdomens into the water while in flight. Odonates demonstrate two types of egg-laying; exophytic and endophytic. Females of species that exhibit exophytic egg-laying (most dragonfly families) fly over the water, stopping at intervals to descend to the surface and tap the abdomen in the water, releasing the cluster of eggs (Corbet, 2004). Species that exhibit endophytic egg-laying (damselflies) deposit eggs into suitable materials on/in the water (Corbet, 2004). Dragonflies have a wide repertoire of flight manoeuvres (Bomphrey et al., 2016). At perches, dragonflies make a series of flight dashes during prey hunting, predation avoidance, and during mate guarding or defending their mating territories (Mischiati et al., 2014). These flight patterns (referred to by respondents as ‘dancing around’) are the reason behind the name *Kyakyanka* (plural - *Akyakyanka*) in the Nchumuru language.

Thirdly, the vernacular names of dragonflies and damselflies are informed by their ecology. For instance, *Saa paga* (wife of rain) in Dagbani depicts the seasonal occurrence of Odonates; they are observed to be abundant in the rainy season or just after but disappear when cloudy or during rains. A similar incidence is recorded by Williams (1960, p140) where the Chinese sometimes refer to Odonates as typhoon flies because they swarm before the occurrence of storms. The variation in seasonal species availability for lotic and lentic species has been made by Kalkman (n.d.). The name *Agyegyensu* (disturb the stillness of water) in Fante depicts the behaviour of a dragonfly hitting the surface of the water body and hence the people believe the sighting of the dragonflies signifies purer or cleaner water. Wyman and

Bailey (1964, p144) also report that dragonflies are depicted as symbols of pure water. Biologically, this act from which the name *Agyegyensu* originates is the exophytic egg-laying behaviour seen in most dragonfly families. Other names such as *Numliaga*, *Bonsuo,* and *Atetensu* also indicate the relationship of Odonates with water bodies. According to Van Damm et al. (2020), the people of Socotra-Yemen have six compound names for Odonata which depict the morphology, behaviour, and habitat.

The non-specificity of Odonate vernacular names has been reported by Cockburn et al. (2014). Despite the names not being species-specific, the name *Agyanka* (orphan) in the Akan language could be referring to males of either the Black-winged widow *Palpopleura lucia* (Drury) or the Shadow-bridge widow, *Palpopleura portia* (Drury). They have black shaded wing patterns (though distinctive) with pruinose abdomen when matured and are common and widespread in Ghana with overlapping habitats. The names *Nkwalaa wiemuhyɛn* and *Gbekɛbiia kɔɔyɔɔmli lɛlɛ* in Akan and Ga respectively depict that children play with Odonates. Dragonflies, as insects played with by children, have been recorded by Damme et al. (2020), Litsinger et al. (2009), and Laurent (2000).

Awareness of the environment (water bodies and forests)

Respondents originating from 11 regions in Ghana opined that Odonates are directly related to water bodies and forests (Table 2). They also demonstrated their awareness of the importance of water bodies and forests (Figure 4). The majority of respondents accorded watershed and source of bush meat as benefits derived from forests. Forests form part of Ghanaian culture to the extent that it is reflected in the language, history, art, and religion (Osei-Owusu and Awotwe-Pratt, 2017). For instance, the Ewe proverb "*Ave bi dzo mexɔa ame ɖe agbe o*" (a burnt forest does not support human life) and the saying by the people of Atewa in the Eastern region of Ghana "*se* kwaeɛ *wua, na Densu ewu*" (the death/destruction of the forest means the death of the Densu river) portray the importance of forests and the reliance of rivers on forests respectively. These two examples illustrate the role of folklore in the environmental management and conservation of natural resources in Ghana (Amlor and Alidza, 2016). Bush meat, which is mainly derived from forests, is an important source of food in Ghana with its trade and consumption estimated to be over US$350 million per year (Ntiamoa-Baidu, 1998).

The respondents were aware of the current environmental threats affecting forests and water bodies in the country. While almost all threats mentioned were human-induced, illegal mining was reported as the most dangerous threat facing water bodies and forests in Ghana. While small-scale mining is an important sector in Ghana, supporting about 4.5 million Ghanaians, the current boost in illegal mining is responsible for the severe damage to water bodies and forests (Boafo, 2019). The devastation caused by illegal mining has resulted in recent calls to halt and ban illegal and small-scale mining in Ghana ("Ghana Sends in Army," 2021). Agriculture is a major economic activity and land use in Ghana. Increasing land use for farming along water bodies is a major concern in Ghana (Ayivor and Gordon, 2012). Infrastructural development, especially around cities over the last decade has resulted in a drastic reduction in vegetation cover (Weeks et al., 2012; Stow et al., 2013).

Local communities enforce laws in the form of taboos (Abayie Boaten, 1998; Attuquayefio and Fobil, 2005). The justification for these protections has been the belief that forests and water bodies serve as homes to ancestral spirits (Diawuo and Issifu, 2015). Respondents mentioned some regulations including, taboo days (days of no activity in forest or water body), the prohibition of unauthorized entry into sacred groves, and the prohibition of hunting and tree cutting in sacred forests, all in the quest to protect and manage forests and water bodies. These are in line with the findings of Boafo et al. (2015) from Northern Ghana. However, the existence of these regulations does not equate to compliance in recent times when the proliferation of western religions has resulted in the downgrade and neglect of indigenous knowledge which was embedded in cultural practices, especially the belief system (Diawuo and Issifu, 2015).

Before adopting an NSBAP, the Ghana pre-tertiary education curricula had very little climate change education (Boakye, 2015; Boateng, 2015). However, the science curriculum covers some aspects of water bodies and some threats facing them, but very little about forests and nothing about biological conservation or wildlife management (CRDD, 2010; NaCCA, 2020). However, the component of forests in Ghanaian folklore outweighs its absence in the formal education curricula. The awareness of the environmental crises or threats facing forest and water bodies can be due to the recent increase in media/press awareness campaigns, self-education, or via life experiences.

Gender and age are important factors in the dynamics of local knowledge (Ayantunde et al., 2008; Guimbo et al., 2011; Magni, 2016) and although there is increasing awareness of their importance (Chiwona-Karltun, et al., 2017), they could vary over time and differ by region. The respondents’ awareness of the state and importance of water bodies and forests was influenced by their age group, gender, education level, and region of origin (Table 4; Figure 3). The distribution of forests and water bodies in the country varies and people in closer associations with forests and water bodies tend to know more and associate more value with them. The recent increase in severity and coverage of illegal mining activities in the country has resulted in a drastic increase in national awareness of the values and threats facing water bodies and forests. Also, one cannot ignore the influence of formal education on peoples’ perception and awareness, especially with the component of forest and water bodies in the national educational curriculum.

As one of the major conservation actions needed to protect Odonates, this study provided us with the opportunity to assess the knowledge base and enlighten the participants on Odonates and invertebrates in general and some aspects of their morphology, ecology, and conservation.

CONCLUSION

Respondents in an urban setting revealed some local knowledge and awareness of dragonflies and damselflies, their ecology, and conservation. They also showed a positive perception of the Odonates which may have been from their own childhood experiences with Odonates. This novel study of Ghanaian perception, local knowledge, and awareness of Odonates has shown that, despite the little attention, the vernacular names for odonates, though not species-specific, have embedded in them significant information on the ecology, morphology and conservation of Odonates. The study has also shown that graduate students in the Greater Accra region of Ghana are aware of the importance and threats of water bodies and forest reserves, in part due to increased formal education in environmental sciences.

In education, the inclusion of locally recognizable fauna and flora in the curriculum and in instruction increases relevance, contextualization, and motivation for learning especially in biological and environmental science education. The identification and naming of insects in local languages are very essential for their recognition and will most likely serve as foundation blocks for promoting their management and biodiversity conservation in general. A nationwide or target-group-specific survey could provide more information on the perceptions, and local knowledge and increase awareness of this important insect group.

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BUTTERFLY ASSEMBLAGES OF TWO WETLANDS: RESPONSE OF BIODIVERSITY TO DIFFERENT ENVIRONMENTAL STRESSORS IN SIERRA LEONE

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ABSTRACT

In a bid to enhance the integrity and health of selected network of ecosystems and effectively manage them in Sierra Leone, a baseline assessment of butterfly diversity of two wetland ecosystems Mamunta Mayosso Wildlife Santuary (MMWS) and Sierra Leone River Estuary (SLRE) affected by different environmental stressors was undertaken as part of the Sierra Leone Wetland Conservation Project (SLWCP). We hypothesised that different environmental stressors affect butterfly communities in wetlands in Sierra Leone and the higher the stress the lower the butterfly diversity in an area. Sampling was conducted via field identification by wing patterns, flight mode, direct counts along transects and charaxes trapping. A total of 2300 individuals representing 95 species of butterflies were recorded. Though butterflies were evenly distributed at both sites, MMWS recorded the highest richness and abundance of butterflies during both seasons. This observation is reported to be because of high environmental stressors such as mining, agriculture, and pollution from factories in the SLRE. The results further show that the MMWS is made up of a mosaic of different vegetation patches that support higher diversity of butterfly species. This study also reveals that anthropogenic activities have a negative impact on butterfly diversity.

BUTTERFLY DIVERSITY: AN INDICATOR FOR ENVIRONMENTAL HEALTH WITHIN TARKWA GOLD MINE, GHANA

Kyerematen, R., Adu-Acheampong, S., **Acquah-Lamptey, D**., Andersen, R. S., Owusu, E. H., Mantey, J.
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ABSTRACT

Many human societies rely on proceeds from mining of metals and fossil fuels for income generation as well as resource supplies from biodiversity. However, these mining activities are in conflict with and threaten the sustainable utilisation and conservation of biodiversity. We used butterflies, a known bioindicator species as surrogates to measure the level of change in vegetation within Tarkwa Gold Mines (TGM) in Ghana. Butterfly assemblages were sampled within the concession and characterised in terms of diversity indices and vegetation type. Transect counts, aerial netting and charaxes trapping were employed to assess butterfly assemblages. Results showed that although there were high records of degraded forest and savanna indicator species, the fairly high presence of deep forested species also shows that some forested areas within the concession are still in good condition. Recommendations are made to maintain forest blocks to serve as refugia for butterflies and urge management to institute measures to restore old and abandoned mined sites. We also recommend policy makers to enact laws that will ensure that, mining organisations lay down plans for sustainable mine operations and biodiversity conservation before being granted license to operate in Ghana.

USING ORTHOPTERA AND HYMENOPTERA INDICATOR GROUPS AS EVIDENCE OF DEGRADATION IN A MINING CONCESSION (TARKWA GOLD MINE) IN GHANA.

Kyerematen, R., Adu-Acheampong, S., **Acquah-Lamptey, D**., Andersen, R. S.

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ABSTRACT

One of the most important bioindicators of change in habitat conditions, especially in tropical Africa, is change in insect diversity. In line with that, the dynamics of Orthoptera and Hymenoptera insect orders were studied and used as evidence of change in ecosystem health after a similar study on Lepidopteran groups revealed some level of degradation in the Tarkwa Gold Mine (TGM). Orthopteran and Hymenopteran species assemblages were sampled within the mine and characterised based on family diversity. Transect counts, sweep netting, malaise trapping, and flight interception trapping methods were employed to sample abundance and diversity of insect assemblages of the above-mentioned insect orders. Results showed that few species belonging to these two orders were recorded within the mine, although the records were dominated by more aggressive and habitat degradation tolerant members as reported for the Lepidopteran group in a previous study. We conclude that records of diversity of these insect orders in this study indicate a reduction in the ecosystem health within TGM. This finding is further proof that there is a general decline in biodiversity within the concession and hence care must be taken to encourage environmentally-friendly mining practices to avoid further degradation. Recommendations are made for environmental management to maintain more natural vegetation to serve as refugia for impacted animals within the concession.

ERKLÄRUNG

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Marburg, den 31. 07. 2022

Daniel Acquah-Lamptey