Title:

DISPERSE: A trait database to assess the dispersal potential of aquatic macroinvertebrates

Authors:

Romain Sarremejane[1]*, Núria Cid[2,3*], Thibault Datry[2], Rachel Stubbington[1], Maria Alp[2], Miguel Cañedo-Argüelles[3], Adolfo Cordero-Rivera[4], Zoltan Csabai[5,6], Cayetano Gutiérrez-Cánovas[7,8], Jani Heino[9], Maxence Forcellini[2], Andrés Millán[10], Amael Paillex[11], Petr Pařil[6], Marek Polášek[5], José Manuel Tierno de Figueroa[12], Philippe Usseglio-Polatera[13], Carmen Zamora-Muñoz[12] & Núria Bonada[3]

[1] School of Science and Technology, Nottingham Trent University, Nottingham NG11 8NS, UK

[2] INRAE, UR RiverLy, centre de Lyon-Villeurbanne, 5 rue de la Doua CS70077, 69626 Villeurbanne Cedex, France

[3] Grup de Recerca Freshwater Ecology, Hydrology and Management (FEHM), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Diagonal 643, 08028 Barcelona, Catalonia, Spain

[4] ECOEVO Lab, E.E. Forestal, Univesidade de Vigo, Campus A Xunqueira, 36005 Pontevedra, Spain

[5]Department of Hydrobiology, University of Pécs, Ifjúság útja 6, H7624 Pécs, Hungary

[6] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 61137 Brno, Czech Republic

[7] Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Braga, Portugal

[8] Institute of Science and Innovation for Bio-Sustainability (IB-S), University of Minho, Braga, Portugal

[9] Finnish Environment Institute, Freshwater Centre, Paavo Havaksen Tie 3, FI-90570 Oulu, Finland

[10] Department of Ecology and Hydrology, Biology Faculty, Murcia University. Campus de Espinardo, 30100. Murcia, Spain

[11] Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Sciences, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland

[12] Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Avenida Fuente Nueva, s/n, 18071 Granada, Spain

[13] Université de Lorraine, CNRS, UMR 7360, LIEC, Laboratoire Interdisciplinaire des Environnements Continentaux, F-57070 Metz, France

*These authors contributed equally to this work.

BIOSKETCH

Many of the authors are members of the European Cooperation in Science and Technology (COST) Action CA15113 Science and Management of Intermittent Rivers and Ephemeral Streams (SMIRES, www.smires.eu), which aims to improve our understanding of intermittent rivers and ephemeral streams (IRES) and translate this into science-based, sustainable management of river networks. One of the main goals of SMIRES is to facilitate sharing of data and experience, bringing together researchers from many disciplines and stakeholders and creating synergies through networking. The dataset provided and analyzed herein reflects

networking and collaboration within the SMIRES working group dedicated to Community Ecology and Biomonitoring.

Abstract

Motivation: Dispersal is an essential process in population and community dynamics but is difficult to measure in the field. In freshwater systems, relevant information on the dispersal of many taxa remains scattered or unpublished, and biological traits related to organisms' morphology, life history and behaviour offer useful dispersal proxies. We compiled information on selected dispersal-related biological traits of European aquatic macroinvertebrates in a unique source: the DISPERSE database. Information within DISPERSE can be used to address fundamental questions in metapopulation ecology, metacommunity ecology, macroecology, and eco-evolutionary research. From an applied perspective, the consideration of dispersal proxies can also improve predictions of ecological responses to global change, and contribute to more effective biomonitoring and conservation management strategies.

Main types of variable contained: Selected macroinvertebrate dispersal-related biological traits: maximum body size, adult female wing length, adult wing pair type, adult life span, number of reproductive cycles per year, lifelong fecundity, dispersal mode (i.e. active, passive, aquatic, aerial), and propensity to drift.

Spatial location: Europe.

Time period: Taxa considered are extant with recent records. Most data were collected in the 20th century and in the period 2000-2019.

Major taxa and level of measurement: Aquatic macroinvertebrates from riverine and lacustrine ecosystems, including Mollusca, Annelida, Platyhelminthes, and Arthropoda such as Crustacea and Insecta. For Insecta, aquatic stages and the aerial (i.e. flying) phases of adults were considered separately. Genus-level taxonomic resolution used, except for some Annelida and Diptera, which are coded at the sub-class, family or sub-family level. In total, the database includes 39 trait categories grouped into nine dispersal-related traits for 480 taxa.

Software format: The data file is in Excel workbook.

KEYWORDS

Aquatic invertebrates, freshwater biodiversity, functional traits, insects, metacommunities, lakes, ponds, proxies, rivers, streams

1. INTRODUCTION

Dispersal is a fundamental ecological process that affects the organization of biological diversity at different temporal and spatial scales (Bohonak & Jenkins, 2003; Clobert, Baguette, Benton, & Bullock, 2012). Dispersal strongly influences metapopulation and metacommunity dynamics through the movement of individuals and species, respectively (Heino et al., 2015). A better understanding of dispersal processes can inform biodiversity management practices (Barton et al., 2015; Heino et al., 2017). However, dispersal itself is difficult to measure, particularly for small organisms, including most invertebrates. Typically, dispersal is measured for single species (e.g. Macneale, Peckarsky, & Likens, 2005; Troast, Suhling, Jinguji, Sahlén, & Ware, 2016) or combinations of few species within one taxonomic group (Arribas et al., 2012; French & McCauley, 2019; Lancaster & Downes, 2017) using methods based on mark and recapture, stable isotopes, or population genetics (Heino et al., 2017; Lancaster & Downes, 2013). Such methods can directly assess dispersal events but are expensive, time-consuming, and thus impractical for studies conducted at the community level or at large spatial scales. In this context, taxon-specific biological traits represent a cost-effective alternative that may serve as proxies for dispersal (Heino et al., 2017; Outomuro & Johansson, 2019; Stevens et al., 2013). These traits interact with landscape structure to determine patterns of effective dispersal (Brown & Swan, 2010; Tonkin et al., 2018).

Aquatic macroinvertebrates inhabiting riverine and lacustrine ecosystems include taxa with diverse dispersal modes and abilities. Moreover, in species with complex life cycles, such as some insects, this diversity is enhanced by distinct differences among life stages. For example, juveniles of many aquatic insects disperse actively or passively in water whereas adults fly over long distances (Wikelski et al., 2006). In all cases, dispersal is affected by multiple traits relating to the morphology (Lancaster & Downes, 2013), life history and behaviour (Clobert et al., 2012) of multiple life stages.

We compiled and harmonised information on dispersal-related traits of aquatic macroinvertebrates across Europe, including both aquatic and aerial (i.e. flying) stages. Although some information on dispersal-related macroinvertebrate traits such as body size, reproduction, locomotion and dispersal mode is available in online databases for European (https://www.freshwaterecology.info/; Schmidt-Kloiber & Hering, 2015; Serra, Cobo, Graça, Dolédec, & Feio, 2016; Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2010) and North American taxa (Vieira et al., 2006), other relevant information is scattered across published literature and unpublished data. Using the expertise of 19 European collaborators, we built a comprehensive database containing nine dispersal-related traits divided into 39 trait categories for 480 taxa. Dispersal-related traits were selected and their trait categories (Table 1) were fuzzy-coded (Chevenet, Dolédec, & Chessel, 1994), following a structure comparable to existing databases (Schmera, Podani, Heino, Erös, & Poff, 2015). Our aim was to provide a single resource facilitating the inclusion of dispersal in ecological, biogeographical and environmental change research, and providing a basis for a global dispersal database.

2. METHODS

Dispersal-related trait selection criteria

We defined dispersal as the unidirectional movement of individuals from one location to another (Bohonak & Jenkins, 2003), assuming that the population-level dispersal rate depends on both the number of dispersers/propagules and dispersers' ability to move across the landscape (Lancaster & Downes, 2017; Lancaster, Downes, & Arnold, 2011).

We selected nine dispersal-related morphological, behavioural and life-history traits. Selected morphological traits were maximum body size, female wing length and wing pair type, the latter two being relevant for flying adult stages of insects. Body size influences organisms' dispersal, especially for active dispersers (Jenkins et al., 2007), with larger animals more

capable of active dispersal over longer distances (e.g. flying adult odonates). In addition, for aquatic stages, body size can be indicative of drift: larger animals drift less (Wilzbach & Cummins, 1989). For flying adults, female wing length was selected because females connect and sustain populations through oviposition, representing adult insects' flying and recolonisation capacity (Graham, Storey, & Smith, 2017): females with larger wings are likely to oviposit farther from their source population (Arribas et al., 2012; Hoffsten, 2004; Rundle, Bilton, & Foggo, 2007). Selected life-history traits were adult life span, life-cycle duration, annual number of reproductive cycles and lifelong fecundity. Adult life span and life-cycle duration respectively reflect the adult (i.e. reproductive) and total life duration, with longer-lived animals typically having more dispersal opportunities (Stevens et al., 2013). The annual number of reproductive cycles and lifelong fecundity were chosen to assess indirect dispersal capacity, i.e. potential propagule production, with multiple reproductive cycles and abundant eggs increasing the expected number of dispersal events. Dispersal behaviour was represented by strategies describing a taxon's predominant dispersal mode (passive, active, aquatic, aerial), and by propensity to drift, which indicates the frequency of flow-mediated passive downstream.

Fuzzy-coding approach and taxonomic resolution

Traits were mostly coded at genus level, but some Diptera and Annelida were coded at family or sub-family level because of their complex taxonomy, identification difficulties and the scarcity of reliable information about their traits. Traits were coded using a fuzzy approach in which a value given to each trait category indicates if the taxon has weak (1), moderate (2) or strong (3) affinity with the category (e.g. Chevenet et al., 1994). This method can incorporate intra-taxonomic variability when trait profiles differ among e.g. species within a genus or within one species in different environments (Bonada & Dolédec, 2018).

Data acquisition, compilation and quality control

Trait information was sourced primarily from the literature by Google Scholar searches using keywords including trait names, synonyms and taxon names, and by searching in existing databases (i.e. https://www.freshwaterecology.info/; Vieira et al., 2006). Altogether, >300 peer-reviewed articles and book chapters were consulted (Table 1). When published information was lacking, traits were coded based on authors' expert knowledge and direct measurements (Table 1). When no European studies were available, we considered information from North America (e.g. Vieira et al., 2006), if experts evaluated traits as comparable across regions (e.g. non-labile traits such as wing pair type do not vary geographically , whereas life-cycle durations may vary across regions). Most traits were coded using multiple sources representing multiple species within a genus. When only one study was available, we supplemented this information with expert knowledge to ensure that trait codes represented the potential variability in the taxon (Table 1).

TABLE 1 Selected dispersal-related aquatic macroinvertebrate traits and the relative contribution of different sources of information (i.e. literature, expert knowledge, direct measurement) used to build the database.

Trait	**Categories**	**Taxa completed (%)**	**Source of information (%)**		
			Literature	**Expert**	**Measured**
Maximum body size (cm)	< 0.25 ≥ 0.25 – 0.5 ≥ 0.5 – 1 ≥ 1 – 2 ≥ 2 – 4 ≥ 4 – 8 ≥ 8	99	100		
Female wing length (insects only) (mm)	< 5 ≥ 5 – 10 ≥ 10 – 15 ≥ 15 – 20	95	57	12	31

Trait	Categories	Taxa completed (%)	Source of information (%)		
			Literature	Expert	Measured
	≥ 20 – 30 ≥ 30 – 40 ≥ 40 – 50 ≥ 50				
Wing pair type (insects only)	1 pair + halters 1 pair + elytra or hemielytra 1 pair + small hind wings 2 similar-sized pairs	100	100		
Life cycle duration	≤ 1 year > 1 year	98	100		
Adult life span	< 1 week ≥ 1 week – 1 month ≥ 1 month – 1 year ≥ 1 year	79	65	35	
Lifelong fecundity	< 100 eggs ≥ 100 – 1000 eggs ≥ 1000 – 3000 eggs ≥ 3000 eggs	75	77	23	
Potential number of reproductive cycles per year	< 1 1 >1	98	100		
Dispersal strategy	Aquatic active Aquatic passive Aerial active Aerial passive	98	100		
Propensity to drift	Rare/catastrophic Occasional Frequent	80	90	10	

3. RESULTS: DESCRIPTION OF THE DATABASE

Sixty-one percent of taxa have complete trait information, with 1-2 traits being incomplete for most remaining taxa (Table 1, Fig. 1). Most of the trait data (88%) originated from published literature and the rest was coded based on expert knowledge and direct measurements of Coleoptera and Heteroptera female wing length (Table 1).

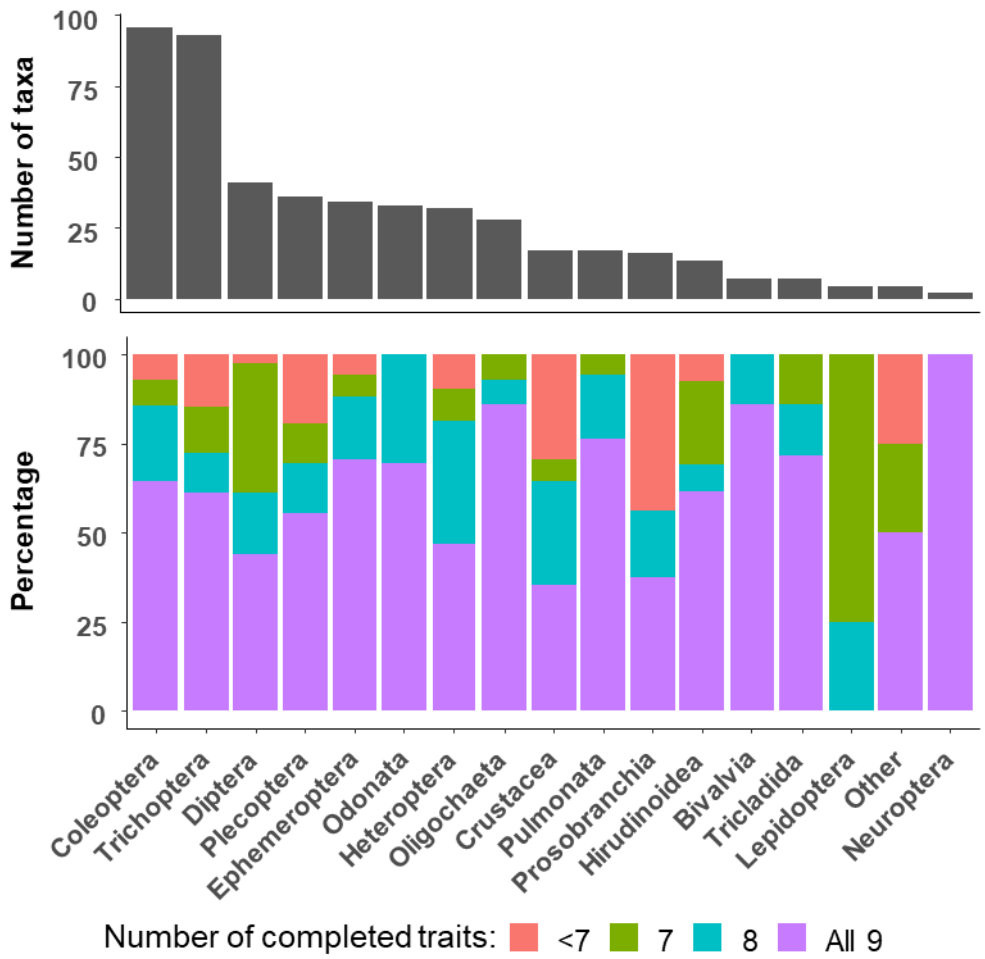

FIGURE 1 Total number of taxa and % of the nine traits completed in each insect order and invertebrate phylum, sub-phylum, class or sub-class. "Other" includes Hydrozoa, Hymenoptera, Megaloptera and Porifera, for which only one taxon is in the database.

Using insects as an example, we performed a fuzzy correspondence analysis (FCA, Chevenet et al., 1994) to visualise and compare differences in trait composition among taxa (Figure 2). Insect groups were clearly divided based on dispersal-related traits, with 32% of the variation explained by the first two FCA axes. Wing pair type and lifelong fecundity had the highest correlation ratios (0.87 and 0.63, respectively) with axis A1, reflecting their clear arrangement along the axis. Wing length (0.73) and maximum size (0.55) best correlated with axis A2 (Figures 2 and S1). For example, Coleoptera typically produce few eggs and have

intermediate body sizes and wing lengths, Odonata produce an intermediate number of eggs and have long wings, and Ephemeroptera produce many eggs and have short wings (Figure 2).

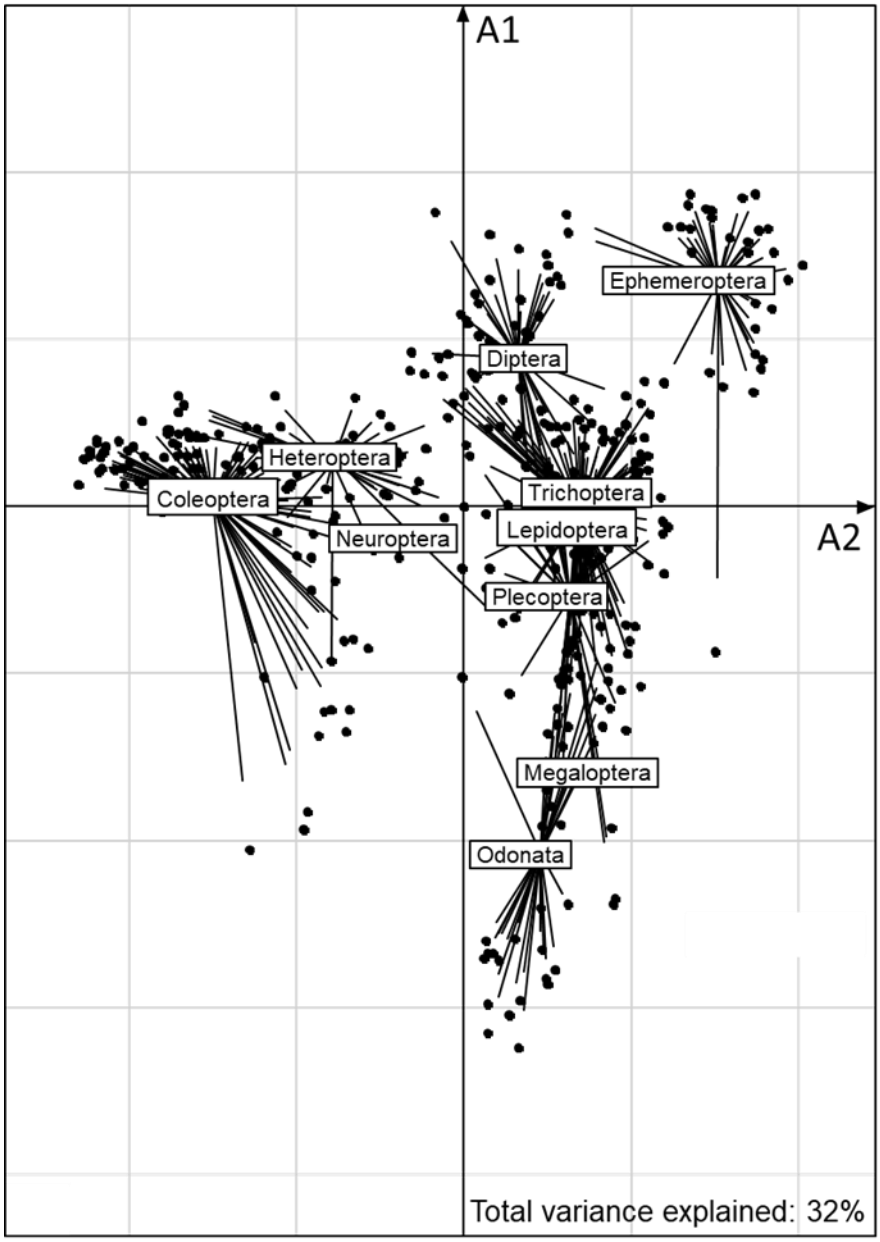

FIGURE 2 Variability in the dispersal-related trait composition of all insect taxa with complete trait profile along fuzzy correspondence analysis axes A1 and A2. Dots indicate taxa and lines converge to the centroid of each taxonomic group/order to depict within-group dispersion.

4. DISCUSSION AND FUTURE PERSPECTIVES

DISPERSE is the first publicly available database describing the dispersal traits of aquatic macroinvertebrates including information on both aquatic and aerial (i.e. flying) life stages. It will promote incorporation of dispersal proxies into fundamental and applied population and community ecology in aquatic ecosystems (Heino et al., 2017). In particular, metacommunity ecology may benefit from the use of dispersal traits (Jacobson & Peres-Neto, 2010; Tonkin et al., 2018), by enabling classification of taxa according to their dispersal potential in more detail than is currently possible. Such classification, used in combination with, for example, spatial distance measurements (Datry, Moya, Zubieta, & Oberdorff, 2016; Sarremejane et al., 2017), may improve understanding of the effects of regional dispersal processes on community assembly and biodiversity patterns. Improved knowledge of taxon-specific dispersal abilities may also inform the design of more effective management practices. For example, recognising dispersal abilities in biomonitoring methods could inform enhanced catchment-scale management strategies that support ecosystems adapting to global change (Cid et al., under review; Datry, Bonada, & Heino, 2016). DISPERSE could also inform conservation strategies by establishing different priorities depending on organisms' dispersal capacities and spatial connectivity (Hermoso, Cattarino, Kennard, Watts, & Linke, 2015). This is especially relevant for highly dynamic freshwater ecosystems, such as temporary rivers and ponds, which repeatedly lose connectivity due to drying, and in which dispersal facilitates populations and community re-establishment after rewetting (Datry, Bonada, et al., 2016).

DISPERSE could also improve species distribution models (SDMs), in which dispersal is rarely considered due to a lack of data (Stevens et al., 2013), limiting the accuracy of model predictions (Thuiller et al., 2013). Recent trait-based approaches have integrated dispersal into SDMs, and DISPERSE could increase model accuracy (Cooper & Soberón,

2018; Willis et al., 2015). Including dispersal in SDMs is especially relevant to assessments of biodiversity loss and species vulnerability to climate change (Bush & Hoskins, 2017; Markovic et al., 2014; Willis et al., 2015). DISPERSE could also advance understanding of eco-evolutionary relationships and biogeographical phenomena. In the context of evolution, groups with lower dispersal abilities should be genetically and taxonomically richer due to long-term isolation (Bohonak, 1999; Dijkstra, Monaghan, & Pauls, 2014). From a biogeographical perspective, regions affected by glaciations should have species with greater dispersal abilities, enabling postglacial recolonisation (Múrria et al., 2017).

By capturing different dispersal-related biological traits, DIPERSE provides information on organisms' potential ability to move between localities as well as on recruitment and reproduction (Tonkin et al., 2018). As an indirect measure of potential but not actual dispersal, traits also facilitate comparison of taxa with different strategies, which could inform studies conducted at large spatial scales, independent of taxonomy (Statzner & Bêche, 2010).

The diverse sources used herein complement existing trait databases by providing new information, most of which would otherwise not be accessible to the scientific community. DISPERSE offers a good coverage of macroinvertebrate groups at the genus level, which is generally considered as adequate to capture biodiversity dynamics (Cañedo-Argüelles et al., 2015; Datry, Melo, et al., 2016; Swan & Brown, 2017; Sarremejane et al., 2017). The database currently represents a Europe-wide resource, which can be updated and expanded as new information becomes available, to include more taxa and traits from across and beyond Europe. DISPERSE lays the foundations for a global trait dispersal database on aquatic taxa, as others have suggested (Maasri, 2019). As freshwater biodiversity declines at unprecedented rates (Reid et al., 2019; Strayer & Dudgeon, 2010), collecting, harmonising and sharing

dispersal-related data on freshwater organisms will underpin evidence-informed initiatives that seek to protect it.

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6. DATA ACCESSIBILITY

DISPERSE is accessible on the Intermittent River Biodiversity Analysis and Synthesis webpage http://irbas.inrae.fr/ for download (as Excel files).

The database is publicly available under a Creative Commons Attribution 4.0 International copyright (CC BY 4.0) and should be appropriately referenced by citing this paper.

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Supporting information

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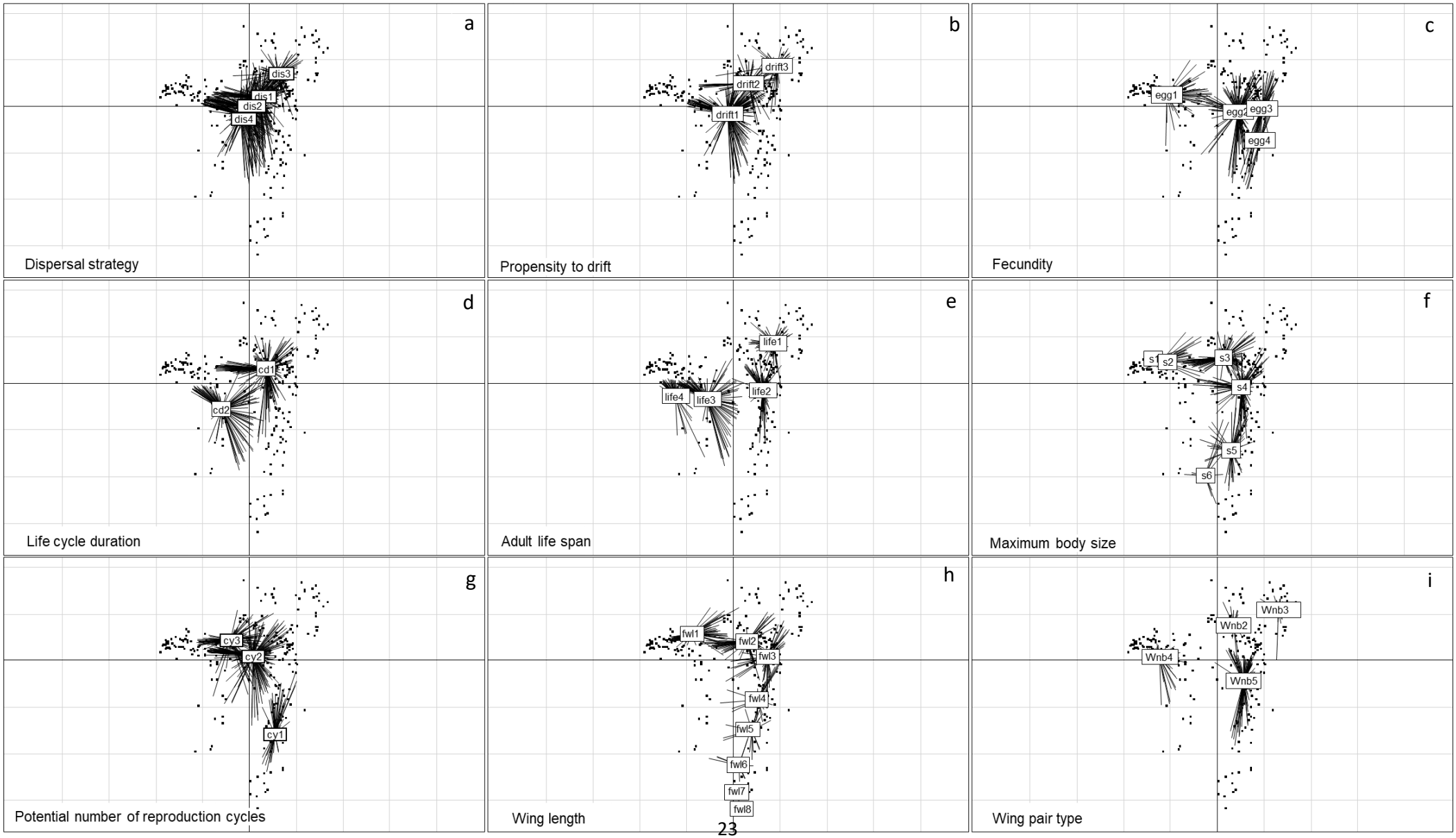
a
dis3
dis1
dis2
dis4
Dispersal strategy
b
drift3
drift2
drift1
Propensity to drift
c
egg1
egg2
egg3
egg4
Fecundity
d
cd1
cd2
Life cycle duration
e
life1
life4
life3
life2
Adult life span
f
s1
s2
s3
s4
s5
s6
Maximum body size
g
cy3
cy2
cy1
Potential number of reproduction cycles
h
fwl1
fwl2
fwl3
fwl4
fwl5
fwl6
fwl7
fwl8
Wing length
i
Wnb3
Wnb2
Wnb4
Wnb5
Wing pair type

Figure S1: Trait category location in the Fuzzy Correspondence Analysis ordination space for each trait: (a) Dispersal strategy = **dis1**: aquatic active, **dis2**: aquatic passive, **dis3**: aerial active, **dis4**: aerial passive; (b) Propensity to drift = **drift1**: rare/catastrophic, **drift2**: occasional, **drift3**: frequent; (c) Fecundity = **egg1**: < 100 eggs, **egg2**: ≥ 100 – 1000 eggs, **egg3**: 1000 – 3000 eggs, **egg4**: ≥ 3000 eggs; (d) Life cycle duration = **cd1**: ≤ 1 year, **cd2**: > 1 year; (e) Adult life span = **life1**: < 1 week, **life2**: ≥ 1 week – 1 month, **life3**: ≥ 1 month – 1 year, **life4**: > 1 year; (f) Maximum body size (cm) = **s1**: < 0.25, **s2**: ≥ 0.25 – 0.5, **s3**: ≥ 0.5 – 1, **s4**: ≥ 1 – 2; **s5**: ≥ 2 – 4, **s6**: ≥ 4 – 8; (g) Potential number of reproductive cycles per year = **cy1**: < 1, **cy2**: 1, **cy3**: > 1; (h) Female wing length (cm) = **fwl1**: < 5, **fwl2**: ≥ 5 – 10, **fwl3**: ≥ 10 – 15, **fwl4**: ≥ 15 – 20, **fwl5**: ≥ 20 – 30, **fwl6**: ≥ 30 – 40, **fwl7**: ≥ 40 – 50, **fwl8**: ≥ 50; (i) Wing pair type = **Wbn2**: 1 pair + halters, **Wbn3**: 1 pair + elytra or hemielytra, **Wbn4**: 1 pair + small hind wings, **Wbn5**: 2 similar-sized pairs.