Title

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

Authors

Romain Sarremejane[1*], Núria Cid[2,3*], Rachel Stubbington[1], Thibault Datry[2], Maria Alp[2], Miguel Cañedo-Argüelles[3], Adolfo Cordero-Rivera[4], Zoltán 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[6], José Manuel Tierno de Figueroa[12], Philippe Usseglio-Polatera[13], Carmen Zamora-Muñoz[12] & Núria Bonada[3]

Affiliations

[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.

Abstract

Dispersal is an essential process in population and community dynamics, but is difficult to measure in the field. In freshwater ecosystems, information on biological traits related to organisms' morphology, life history and behaviour provides useful dispersal proxies, but information remains scattered or unpublished for many taxa. We compiled information on multiple dispersal-related biological traits of European aquatic macroinvertebrates in a unique resource, the DISPERSE database. DISPERSE includes 39 trait categories grouped into nine dispersal-related traits for 480 taxa, including Annelida, Mollusca, Platyhelminthes, and Arthropoda such as Crustacea and Insecta, generally at the genus level. Information within DISPERSE can be used to address fundamental questions in metapopulation ecology, metacommunity ecology, macroecology and evolutionary ecology research. Information on dispersal proxies can be applied to improve predictions of ecological responses to global change, and to inform improvements to biomonitoring and conservation management strategies. The diverse sources used in DISPERSE complement existing trait databases by providing new information on dispersal traits, most of which would not otherwise be accessible to the scientific community.

Background & Summary

Dispersal is a fundamental ecological process that affects the organization of biological diversity at multiple temporal and spatial scales[1,2]. Dispersal strongly influences metapopulation and metacommunity dynamics through the movement of individuals and species, respectively[3]. A better understanding of dispersal processes can inform biodiversity management practices[4,5]. However, dispersal is difficult to measure directly, particularly for small organisms, including most invertebrates[6]. Typically, dispersal is measured for single species[7,8] or combinations of few species within one taxonomic group[9–11], using methods based on mark and recapture, stable isotopes, or population genetics[5,12]. 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[5,6,13,14]. These traits interact with landscape structure to determine patterns of effective dispersal[15,16].

Aquatic macroinvertebrates inhabiting freshwater ecosystems include taxa with diverse dispersal modes and abilities (Figure 1). For species with complex life cycles, such as some insects, this diversity is enhanced by distinct dispersal strategies among life stages. For example, juveniles of many aquatic insects disperse actively and/or passively in water whereas adults fly over land[17]. In any case, dispersal is affected by multiple traits relating to the morphology[6,12], life history and behaviour[2] of different life stages.

We compiled and harmonized information on dispersal-related traits of aquatic macroinvertebrates from across Europe, including both aquatic and aerial (i.e. flying) stages. Although information on some dispersal-related traits such as body size, reproduction, locomotion and dispersal mode is available in online databases for European[18–20] and North American taxa[21], other relevant information is scattered across published literature and unpublished data. Using the expertise of 19 experts, we built a comprehensive database containing nine dispersal-related traits divided into 39

trait categories for 480 European taxa. Dispersal-related traits were selected and their trait categories fuzzy-coded[22] following a structure comparable to existing databases[23]. Our aim was to provide a single resource facilitating the inclusion of dispersal in ecological research, and to create the basis for a global dispersal database.

Methods

Dispersal-related trait selection criteria

We defined dispersal as the unidirectional movement of individuals from one location to another[1], assuming that population-level dispersal rates depend on both the number of dispersers/propagules and dispersers' ability to move across the landscape[11,24].

We selected nine dispersal-related morphological, behavioural and life-history traits (Table 1). Selected morphological traits were maximum body size, female wing length and wing pair type, the latter two relating only to flying adult insects. Body size influences organisms' dispersal[6], especially for active dispersers[25], with larger animals more capable of active dispersal over longer distances (e.g. flying adult dragonflies[6]). Wing morphology, and in particular wing length, is related to the dispersal of flying adult insects[6,26]. Female wing length was selected because females connect and sustain populations through oviposition, thus representing adult insects' flying and recolonization capacity[27]. Females with larger wings are likely to oviposit farther from their source population[6,10,28]. We also described wing morphology as insect wing types, i.e. one or two pairs of wings, and the presence of halters, elytra or hemielytra, or small hind wings[12] (Figure 1). 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[13]. The annual number of reproductive cycles and lifelong fecundity assess dispersal capacity based on potential propagule production, with multiple reproductive cycles and abundant eggs increasing the expected number of dispersal events[6]. Dispersal behaviour was represented by a taxon's predominant

100 dispersal mode (passive and/or active, aquatic and/or aerial), and by propensity to drift, which
101 indicates the frequency of flow-mediated passive downstream dispersal.

102 *Data acquisition and compilation*

103 A taxa list was generated based on existing trait databases[20] and modified to reflect current
104 taxonomic classifications. Trait information was sourced primarily from the literature using Google
105 Scholar searches of keywords including trait names, synonyms and taxon names, and by searching in
106 existing databases[18,21]. Altogether, >300 peer-reviewed articles and book chapters were consulted
107 (Supplementary File 1). When no European studies were available, we considered information from
108 other continents only if experts evaluated traits as comparable across regions. When published
109 information was lacking, traits were coded based on authors' expert knowledge and direct
110 measurements. Specifically, for 139 species in 69 genera of Coleoptera and Heteroptera, female wing
111 lengths were characterized using measurements of 538 individuals in experts' reference collections,
112 sampled in Finland, Hungary and Greece. The number of species measured within a genus varied
113 between 1 and 10 in proportion to the number of species within each genus in Europe. For example,
114 for the most specious genera, common and rare species as well as northern latitude and
115 Mediterranean species were included.

116 *Fuzzy-coding approach and taxonomic resolution*

117 Traits were coded using a fuzzy approach in which a value given to each trait category indicates if the
118 taxon has no (0), weak (1), moderate (2) or strong (3) affinity with the category[22]. This method can
119 incorporate intra-taxon variability when trait profiles differ among e.g. species within a genus, early
120 and late instars, or within one species in different environments[29]. Most traits were coded at genus
121 level, but some Diptera and Annelida were coded at family, sub-families or tribe level because of
122 their complex taxonomy, identification difficulties and the scarcity of reliable information about their
123 traits.

Data Records

DISPERSE can be downloaded as an Excel spreadsheet from the Intermittent River Biodiversity Analysis and Synthesis webpage[30] or Figshare at: https://figshare.com/s/4f074fb4bdbbe8cf149e.

The database comprises three sheets: DataKey, Data and Reference list. The "Datakey" sheet summarizes the content of each column in the "Data" sheet. The "Data" sheet includes the fuzzy-coded trait categories and cites the sources used to code each trait. The four first columns list the taxa and their taxonomy (group, family, genus [or lowest taxonomic resolution achieved including e.g. tribes and sub-families] and genus synonyms) to allow users to sort and compile information. Sources are cited in chronological order by the surname of the first author and the year of publication. Expert evaluations are reported as "Unpublished" followed by the name of the expert providing the information. Direct measurements are reported as "Direct measurement from" followed by the expert's name. The "Reference list" sheet contains the references cited in the "Data" sheet, organized in alphabetical order and then by date (also available in Supplementary File 1).

In total, the database contains nine dispersal-related traits divided into 39 trait categories for 480 taxa. Most (78%) taxa are insects, principally Coleoptera and Trichoptera, as these are, together with Diptera, the most diverse orders in freshwater ecosystems[31]. DISPERSE provides complete trait information for 61% of taxa, with 1-2 traits being incomplete for the 39% remaining taxa (Table 1, Figure 2). The traits with the highest percentage of information across taxa were wing pair type and maximum body size, followed by dispersal strategy, life-cycle duration, potential number of reproductive cycles per year, and female wing length (Table 1). The percentage of completed information was lower for two life-history traits: adult lifespan and lifelong fecundity (Table 1).

Technical Validation

Most of the trait information (88%) originated from published literature (Supplementary File 1) and the rest was coded based on expert knowledge (9%) and direct measurements (3%) (Table 1). The database states information sources for each trait and taxon, allowing users evaluate data quality.

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 potential variability in the taxon.

Using insects as an example, we performed a fuzzy correspondence analysis (FCA)[22] to visualize variability in trait composition among taxa (Figure 3). Insect orders were clearly distinguished based on their 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 coefficient (0.87 and 0.63, respectively) with axis A1. Female wing length (0.73) and maximum body size (0.55) best correlated with axis A2 (Figures 3 and 4). For example, Coleoptera typically produce few eggs and have intermediate maximum 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 (Figures 1 and 4).

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. For example, additional information could be collected on other measures of wing morphology[10,14] and functionality or descriptors of exogenous dispersal vectors such as wind and animals[32]. DISPERSE lays the foundations for a global dispersal trait database, the lack of which is recognized as limiting research progress across multiple disciplines[33].

Usage Notes

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 provides good coverage of macroinvertebrates at the genus level, which is generally considered as adequate to capture biodiversity dynamics[34–37]. It will promote incorporation of dispersal proxies into fundamental and applied population and community ecology in aquatic ecosystems[5]. In particular, metacommunity ecology may benefit from the use of dispersal traits[15,38], which enable classification

174 of taxa according to their dispersal potential in more detail. Such classification, used in combination
175 with, for example, spatial distance measurements[39,40], may advance our understanding of the effects
176 of regional dispersal processes on community assembly and biodiversity patterns. Improved
177 knowledge of taxon-specific dispersal abilities may also inform the design of more effective
178 management practices. For example, recognizing dispersal abilities in biomonitoring methods could
179 inform enhancements to catchment-scale management strategies that support ecosystems adapting
180 to global change[41,42]. DISPERSE could also inform freshwater conservation strategies by establishing
181 different priorities depending on organisms' dispersal capacities in relation to spatial connectivity[43].

182 DISPERSE could also improve species distribution models (SDMs), in which dispersal has
183 rarely been considered due to insufficient data [13], limiting the accuracy of model predictions[44].
184 Recent trait-based approaches have begun to integrate dispersal into SDMs, and DISPERSE could
185 increase model accuracy[45,46]. Including dispersal in SDMs is especially relevant to assessments of
186 biodiversity loss and species vulnerability to climate change[45,47,48]. DISPERSE could also advance
187 understanding of eco-evolutionary relationships and biogeographical phenomena. In an evolutionary
188 context, groups with lower dispersal abilities should be genetically and taxonomically richer due to
189 long-term isolation[49,50]. From a biogeographical perspective, regions affected by glaciations should
190 have species with greater dispersal abilities, enabling postglacial recolonization[51].

191 By capturing different dispersal-related biological traits, DISPERSE provides information on
192 organisms' potential ability to move between localities as well as on recruitment and reproduction[15].
193 Traits also facilitate comparison of taxa with different dispersal strategies, which could inform studies
194 conducted at large spatial scales, independent of taxonomy[52].

195 Users should note that dispersal-related traits included in DISPERSE represent an indirect
196 measure of dispersal, not actual dispersal. Therefore, the database is not intended to substitute
197 population-level studies related to dispersal, but to act as a repository that collates and summarizes
198 information from such studies. As freshwater biodiversity declines at unprecedented rates[53,54],

collecting, harmonizing and sharing dispersal-related data on freshwater organisms will underpin evidence-informed initiatives that seek to support the resilience of ecosystems adapting to global change.

Acknowledgements

The study was supported by the COST Action CA15113 Science and Management of Intermittent Rivers and Ephemeral Streams (http://www.smires.eu/), funded by COST (European Cooperation in Science and Technology). NC was supported by the French research program Make Our Planet Great Again. MC-A was supported by the MECODISPER project (CTM2017-89295-P) funded by the Spanish Ministerio de Economía, Industria y Competitividad (MINECO) - Agencia Estatal de Investigación (AEI) and cofunded by the European Regional Development Fund (ERDF). AC-R acknowledges funding by MINECO-AEI-ERDF (CGL2014-53140-P). CG-C was supported by the EDRF (COMPETE2020 and PT2020) and the Portuguese Foundation for Science and Technology, through the CBMA strategic program UID/BIA/04050/2019 (POCI-01-0145-FEDER-007569) and the STREAMECO project (Biodiversity and ecosystem functioning under climate change: from the gene to the stream, PTDC/CTA-AMB/31245/2017). PP and MP were supported by the Czech Science Foundation (P505-20-17305S). ZC was supported by the projects EFOP-3.6.1.-16-2016-00004, 20765-3/2018/FEKUTSTRAT and TUDFO/47138/2019-ITM.

Author contributions

NB, NC and RSa developed the idea and data collection framework. RSa compiled most of the dispersal-related trait data and structured the database. All authors contributed to the addition and checking of information included in the database, and ZC provided direct measurements of several taxa. AC-R designed Figure 1. MA, MC-A, CG-C and MF helped to finalize the database reference list.

NC wrote the first draft of the manuscript, and all authors contributed to finalizing it. RSt proofread the manuscript.

Competing interests

The authors declare no competing interests.

References

1. Bohonak, A. J. & Jenkins, D. G. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.* **6**, 783–796 (2003).

2. Clobert, J., Baguette, M., Benton, T. G. & Bullock, J. M. *Dispersal ecology and evolution*. (Oxford Univ. Press, 2012).

3. Heino, J. *et al.* Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshw. Biol.* **60**, 845–869 (2015).

4. Barton, P. S. *et al.* Guidelines for using movement science to inform biodiversity policy. *Environ. Manage.* **56**, 791–801 (2015).

5. Heino, J. *et al.* Integrating dispersal proxies in ecological and environmental research in the freshwater realm. *Environ. Rev.* **25**, 334–349 (2017).

6. Rundle, S. D., Bilton, D. T. & Foggo, A. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. in *Body Size: The Structure and Function of Aquatic Ecosystems* (eds. Hildrew, A. G., Raffaelli, D. G. & Edmonds-Brown, R.) 186–209 (Cambridge Univ. Press, 2007).

7. Macneale, K. H., Peckarsky, B. L. & Likens, G. E. Stable isotopes identify dispersal patterns of stonefly populations living along stream corridors. *Freshw. Biol.* **50**, 1117–1130 (2005).

8. Troast, D., Suhling, F., Jinguji, H., Sahlén, G. & Ware, J. A global population genetic study of *Pantala flavescens*. *PLoS One* **11**, 1–13 (2016).

246 9. French, S. K. & McCauley, S. J. The movement responses of three libellulid dragonfly species to
247 open and closed landscape cover. *Insect Conserv. Divers.* (2019). doi:10.1111/icad.12355

248 10. Arribas, P. *et al.* Dispersal ability rather than ecological tolerance drives differences in range
249 size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *J. Biogeogr.* **39**, 984–
250 994 (2012).

251 11. Lancaster, J. & Downes, B. J. Dispersal traits may reflect dispersal distances, but dispersers
252 may not connect populations demographically. *Oecologia* **184**, 171–182 (2017).

253 12. Lancaster, J. & Downes, B. J. Dispersal in the terrestrial environment. in *Aquatic Entomology*
254 (eds. Lancaster, J. & Downes, B. J.) 137–153 (Oxford Univ. Press, 2013).

255 13. Stevens, V. M. *et al.* Dispersal syndromes and the use of life-histories to predict dispersal.
256 *Evol. Appl.* **6**, 630–642 (2013).

257 14. Outomuro, D. & Johansson, F. Wing morphology and migration status, but not body size,
258 habitat or Rapoport's rule predict range size in North-American dragonflies (Odonata:
259 Libellulidae). *Ecography* **42**, 309–320 (2019).

260 15. Tonkin, J. D. *et al.* The role of dispersal in river network metacommunities: patterns,
261 processes, and pathways. *Freshw. Biol.* **63**, 141–163 (2018).

262 16. Brown, B. L. & Swan, C. M. Dendritic network structure constrains metacommunity properties
263 in riverine ecosystems. *J. Anim. Ecol.* **79**, 571–580 (2010).

264 17. Wikelski, M. *et al.* Simple rules guide dragonfly migration. *Biol. Lett.* **2**, 325–329 (2006).

265 18. Schmidt-Kloiber, A. & Hering, D. www.freshwaterecology.info – An online tool that unifies,
266 standardises and codifies more than 20,000 European freshwater organisms and their
267 ecological preferences. *Ecol. Indic.* **53**, 271–282 (2015).

268 19. Serra, S. R. Q., Cobo, F., Graça, M. A. S., Dolédec, S. & Feio, M. J. Synthesising the trait

269 information of European Chironomidae (Insecta: Diptera): towards a new database. *Ecol.*
270 *Indic.* **61**, 282–292 (2016).

271 20. Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. *Invertébrés d'Eau Douce:*
272 *Systématique, Biologie, Écologie*. (CNRS Éditions, 2010).

273 21. Vieira, N. K. M. *et al. A Database of Lotic Invertebrate Traits for North America. U.S. Geological*
274 *Survey Data Series 187* (2006).

275 22. Chevenet, F., Dolédec, S. & Chessel, D. A fuzzy coding approach for the analysis of long-term
276 ecological data. *Freshw. Biol.* **31**, 295–309 (1994).

277 23. Schmera, D., Podani, J., Heino, J., Erös, T. & Poff, N. L. R. A proposed unified terminology of
278 species traits in stream ecology. *Freshw. Sci.* **34**, 823–830 (2015).

279 24. Lancaster, J., Downes, B. J. & Arnold, A. Lasting effects of maternal behaviour on the
280 distribution of a dispersive stream insect. *J. Anim. Ecol.* **80**, 1061–1069 (2011).

281 25. Jenkins, D. G. *et al.* Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.* **16**, 415–425
282 (2007).

283 26. Harrison, R. G. Dispersal polymorphisms in insects. *Annu. Rev. Ecol. Syst.* **11**, 95–118 (1980).

284 27. Graham, E. S., Storey, R. & Smith, B. Dispersal distances of aquatic insects: upstream crawling
285 by benthic EPT larvae and flight of adult Trichoptera along valley floors. *New Zeal. J. Mar.*
286 *Freshw. Res.* **51**, 146–164 (2017).

287 28. Hoffsten, P. O. Site-occupancy in relation to flight-morphology in caddisflies. *Freshw. Biol.* **49**,
288 810–817 (2004).

289 29. Bonada, N. & Dolédec, S. Does the Tachet trait database report voltinism variability of aquatic
290 insects between Mediterranean and Scandinavian regions? *Aquat. Sci.* **80**, 1–11 (2018).

291 30. Sarremejane, R. *et al.* DISPERSE: a trait database to assess the dispersal potential of aquatic

292 macroinvertebrates. *Intermittent River Biodiversity Analysis and Synthesis* (2020). Available at:
293 http://irbas.inrae.fr/latest-news/disperse-database-sarremejane-et-al-2020.

294 31. Lévêque, C., Balian, E. V & Martens, K. An assessment of animal species diversity in
295 continental waters. *Hydrobiologia* **542**, 39–67 (2005).

296 32. Green, A. J. & Figuerola, J. Recent advances in the study of long-distance dispersal of aquatic
297 invertebrates via birds. *Divers. Distrib.* **11**, 149–156 (2005).

298 33. Maasri, A. A global and unified trait database for aquatic macroinvertebrates: the missing
299 piece in a global approach. *Front. Environ. Sci.* **7**, 1–3 (2019).

300 34. Cañedo-Argüelles, M. *et al.* Dispersal strength determines meta-community structure in a
301 dendritic riverine network. *J. Biogeogr.* **42**, 778–790 (2015).

302 35. Datry, T. *et al.* Metacommunity patterns across three Neotropical catchments with varying
303 environmental harshness. *Freshw. Biol.* **61**, 277–292 (2016).

304 36. Swan, C. M. & Brown, B. L. Metacommunity theory meets restoration: isolation may mediate
305 how ecological communities respond to stream restoration. *Ecol. Appl.* **27**, 2209–2219 (2017).

306 37. Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J. & Muotka, T. Habitat connectivity and
307 dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river
308 networks. *Freshw. Biol.* **62**, 1073–1082 (2017).

309 38. Jacobson, B. & Peres-Neto, P. R. Quantifying and disentangling dispersal in metacommunities:
310 How close have we come? How far is there to go? *Landsc. Ecol.* **25**, 495–507 (2010).

311 39. Sarremejane, R. *et al.* Do metacommunities vary through time? Intermittent rivers as model
312 systems. *J. Biogeogr.* **44**, 2752–2763 (2017).

313 40. Datry, T., Moya, N., Zubieta, J. & Oberdorff, T. Determinants of local and regional
314 communities in intermittent and perennial headwaters of the Bolivian Amazon. *Freshw. Biol.*

315 **61**, 1335–1349 (2016).

316 41. Cid, N. *et al.* A metacommunity approach to improve biological assessments in highly dynamic
317 freshwater ecosystems. *Bioscience* **70**, 427–438 (2020).

318 42. Datry, T., Bonada, N. & Heino, J. Towards understanding the organisation of
319 metacommunities in highly dynamic ecological systems. *Oikos* **125**, 149–159 (2016).

320 43. Hermoso, V., Cattarino, L., Kennard, M. J., Watts, M. & Linke, S. Catchment zoning for
321 freshwater conservation: refining plans to enhance action on the ground. *J. Appl. Ecol.* **52**,
322 940–949 (2015).

323 44. Thuiller, W. *et al.* A road map for integrating eco-evolutionary processes into biodiversity
324 models. *Ecol. Lett.* **16**, 94–105 (2013).

325 45. Willis, S. G. *et al.* Integrating climate change vulnerability assessments from species
326 distribution models and trait-based approaches. *Biol. Conserv.* **190**, 167–178 (2015).

327 46. Cooper, J. C. & Soberón, J. Creating individual accessible area hypotheses improves stacked
328 species distribution model performance. *Glob. Ecol. Biogeogr.* **27**, 156–165 (2018).

329 47. Markovic, D. *et al.* Europe's freshwater biodiversity under climate change: distribution shifts
330 and conservation needs. *Divers. Distrib.* **20**, 1097–1107 (2014).

331 48. Bush, A. & Hoskins, A. J. Does dispersal capacity matter for freshwater biodiversity under
332 climate change? *Freshw. Biol.* **62**, 382–396 (2017).

333 49. Bohonak, A. J. Dispersal, gene flow, and population structure. *Q. Rev. Biol.* **74**, 21–45 (1999).

334 50. Dijkstra, K.-D. B., Monaghan, M. T. & Pauls, S. U. Freshwater biodiversity and aquatic insect
335 diversification. *Annu. Rev. Entomol.* **59**, 143–163 (2014).

336 51. Múrria, C. *et al.* Local environment rather than past climate determines community
337 composition of mountain stream macroinvertebrates across Europe. *Mol. Ecol.* **26**, 6085–6099

(2017).

52. Statzner, B. & Bêche, L. A. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshw. Biol.* **55**, 80–119 (2010).

53. Strayer, D. L. & Dudgeon, D. Freshwater biodiversity conservation: recent progress and future challenges. *J. North Am. Benthol. Soc.* **29**, 344–358 (2010).

54. Reid, A. J. *et al.* Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **94**, 849–873 (2019).

346 ## Figures and Tables

347 **Table 1** Dispersal-related aquatic macroinvertebrate traits included in the DISPERSE database and the
348 relative contribution of different sources of information (i.e. literature, expert knowledge, direct
349 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 ≥ 20 – 30 ≥ 30 – 40 ≥ 40 – 50 ≥ 50	95	57	12	31
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	Aquatic active	98	100		

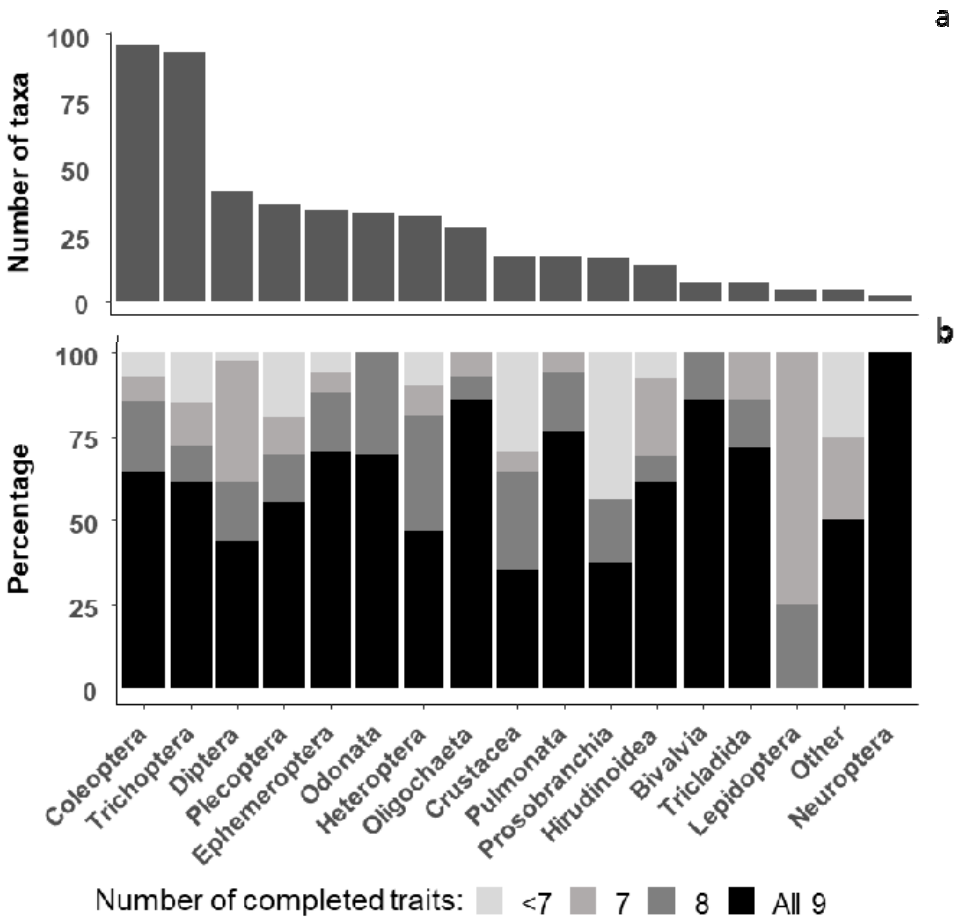
Trait	Categories	Taxa	Source of information (%)		
strategy	Aquatic passive				
	Aerial active				
	Aerial passive				
Propensity to drift	Rare/catastrophic				
	Occasional	80	90	10	
	Frequent				
All traits		61	88	9	3

Figure 1. The dispersal-related trait diversity of aquatic macroinvertebrates. Taxa that disperse in water include the crustaceans *Potamon* (a) and *Asellus* (red arrow in b), planarians (b), the bivalve mollusc *Unio* (c), insect larvae such as the Diptera genus *Simulium* (d) and Plecoptera genus *Leuctra* (e), and adult Coleoptera including dytiscid *Cybister* (f). Such aquatic dispersers may move passively in the drift (c, d) and/or actively crawl or swim (a, b, e, f). Most adult insects have wings and can fly overland (f-n). Wings are morphologically diverse and include various types: one wing pair, as in Diptera such as the syrphid genus *Eristalis* (g); one pair of wings with elytra for Coleoptera including the genus *Enochrus* (h) or with hemielytra for Heteroptera such as the genus *Hesperocorixa* (i); two wing pairs including one pair of small hind wings for Ephemoptera including the genus *Ephemera* (j); and two pairs of similar-sized wings for species such as the Trichoptera genus *Polycentropus* (k), the Megaloptera genus *Sialis (l)* or the Odonata genera *Ischnura* (m) and *Crocothemis* (n). Wings range in size from a few mm in some Diptera (g) up to more than 3 cm (l-n), with the Odonata exemplifying the large morphologies. Taxa vary in the number of eggs produced per individual, ranging from tens

366 per reproduction cycle for most Coleoptera and Heteroptera such as the genus *Sigara* (o) to several
367 hundreds in the egg masses of most Ephemeroptera and Trichoptera, such as those of the genus
368 *Hydropsyche* (p). Credits: Adolfo Cordero-Rivera (a-g, i, k-n), Jesús Arribas (h), Pere Bonada (j), José
369 Antonio Carbonell (o) and Maria Alp (p).

370

371



372

373 **Figure 2.** Total number of taxa and percentage of the nine traits completed in each insect order and

374 macroinvertebrate phylum, sub-phylum, class or sub-class. "Other" includes Hydrozoa,

375 Hymenoptera, Megaloptera and Porifera, for which the database includes only one genus.

376

377

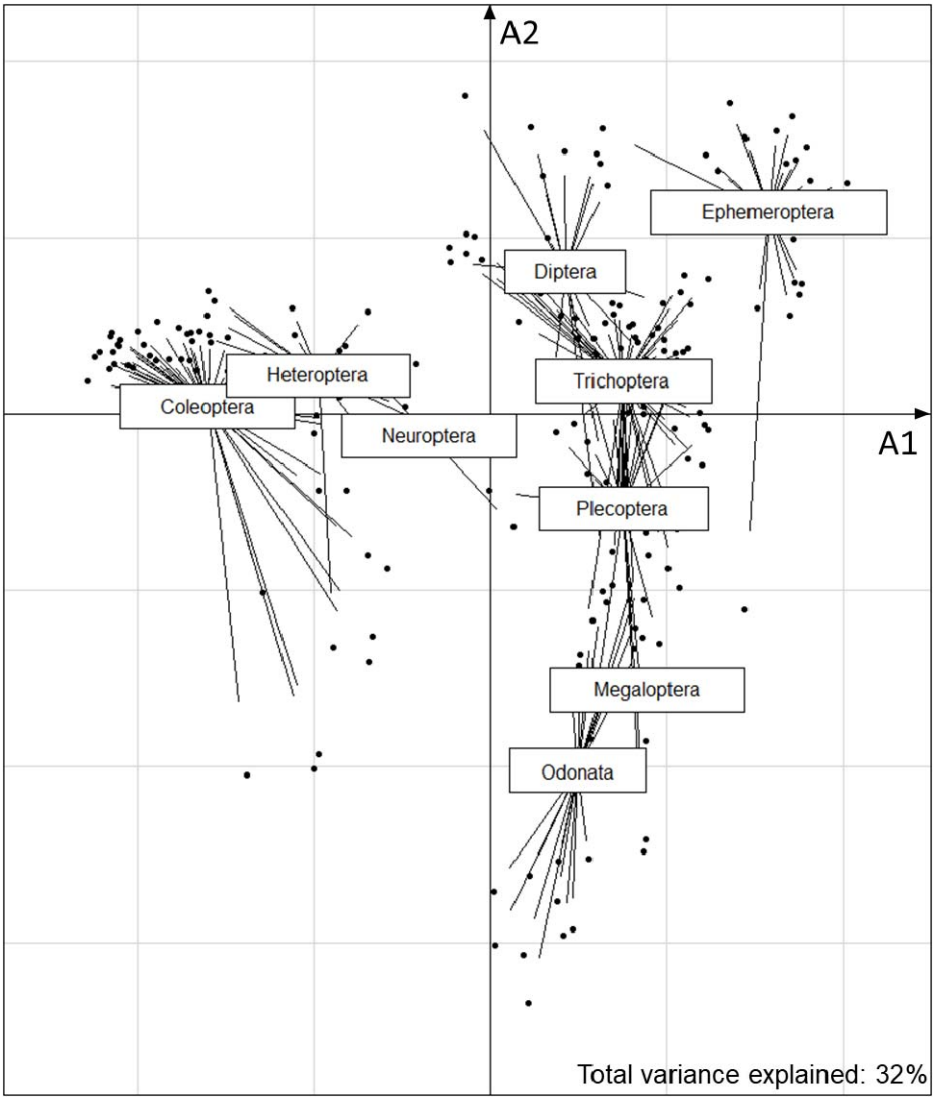
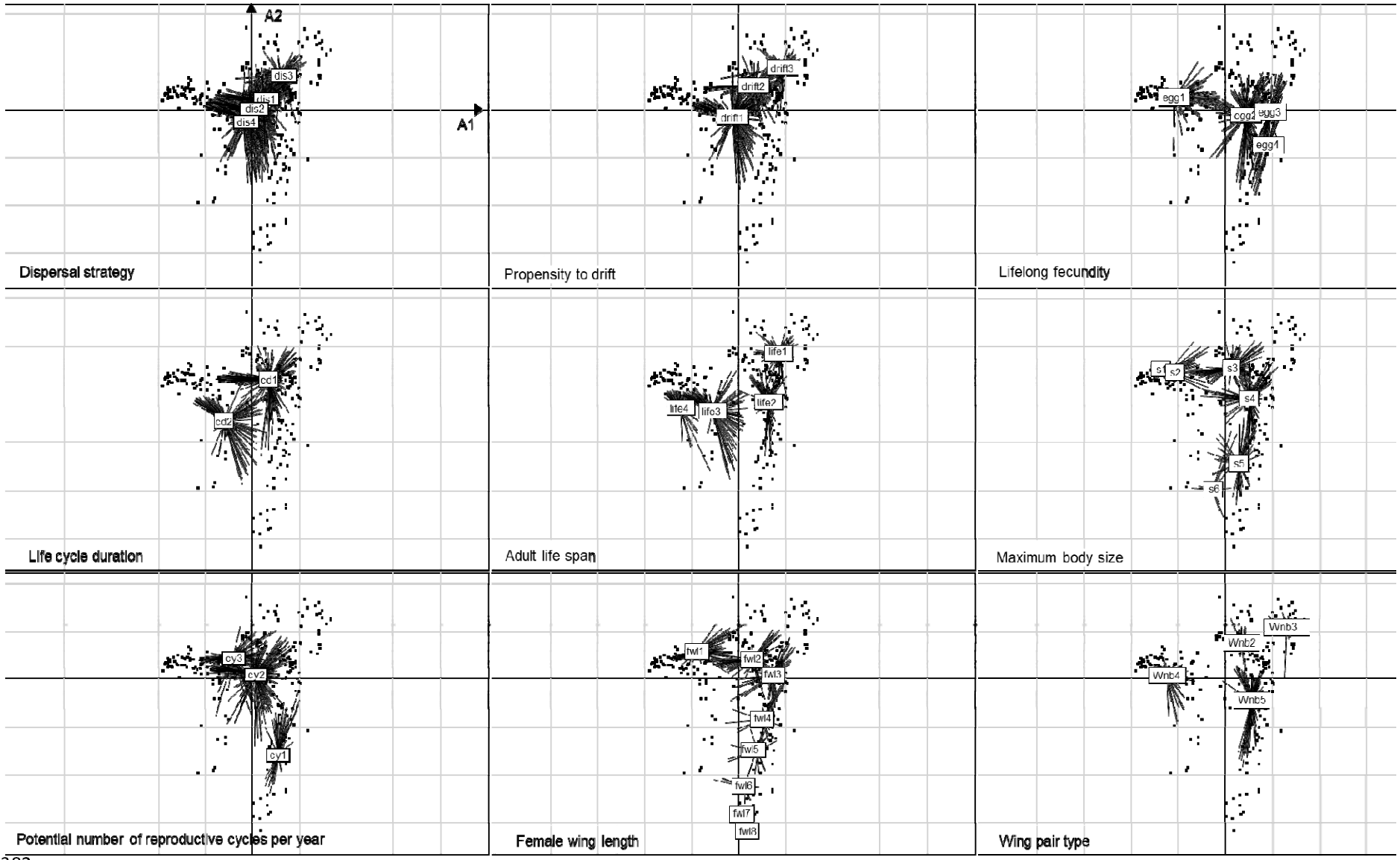


Figure 3. Variability in the dispersal-related trait composition of all insect orders with complete trait profiles along fuzzy correspondence analysis axes A1 and A2. Dots indicate taxa and lines converge to the centroid of each order to depict within-group dispersion.


A2
A1
dis3
dis1
dis2
dis4
Dispersal strategy
drift3
drift2
drift1
Propensity to drift
egg1
egg3
egg1
Lifelong fecundity
cd1
cd2
Life cycle duration
life1
life4
life3
life2
Adult life span
s1
s2
s3
s4
s5
s6
Maximum body size
cv3
cv2
cv1
Potential number of reproductive cycles per year
fwl1
fwl2
fwl3
fwl4
fwl5
fwl6
fwl7
fwl8
Female wing length
Wnb3
Wnb2
Wnb4
Wnb5
Wing pair type

382

a

b

Figure 4. Trait category locations 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.

391

392 **SUPPORTING INFORMATION**

393 **Supplementary File 1.** List of references used to build DISPERSE.

394

395

396