Integrating dispersal proxies in ecological and environmental research in the freshwater realm

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33 ABSTRACT

34 Dispersal is one of the key mechanisms affecting the distribution of individuals, populations

35 and communities in nature. Despite advances in the study of single species, it has been

36 notoriously difficult to account for dispersal in multispecies metacommunities, where it

37 potentially has strong effects on community structure beyond those of local environmental

38 conditions. Dispersal should thus be directly integrated in both basic and applied research by

39 using proxies. Here, we review the use of proxies in the current metacommunity research,

40 suggest new proxies and discuss how proxies could be used in community modelling,

41 particularly in freshwater systems. We suggest that while traditional proxies may still be

42 useful, proxies formerly utilized in transport geography may provide useful novel insights

43 into the structuring of biological communities in freshwater systems. We also suggest that

44 understanding the utility of such proxies for dispersal in metacommunities is highly important

45 for many applied fields, such as freshwater bioassessment, conservation planning and

46 recolonization research in the context of restoration ecology. These research fields have often

47 ignored spatial dynamics, and focused mostly on local environmental conditions and changes

48 therein. Yet, the conclusions of these applied studies may change considerably if dispersal is

49 taken into account.

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Introduction

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Ever since Charles Darwin, ecologists have been interested in dispersal (Ridley 2004), i.e., the movement of an organism from one location to another. Dispersal is one of the most important mechanisms affecting the distribution of individuals, populations and communities (Baguette et al. 2013; Lowe and McPeek 2014). At the same time, dispersal is also one of the most difficult phenomena to study even for a single individual or a single species in nature (Bilton et al. 2001; Nathan et al. 2008). The problem is exacerbated for dozens to hundreds of species in a metacommunity, i.e., a set of local communities connected by dispersal (Leibold et al. 2004), making it virtually impossible to account for dispersal directly for such large number of entities in natural settings. Ecologists have therefore relied on various proxies, which are assumed to relate to the effects of dispersal on community structure (Jacobson and Peres-Neto 2010; Jones et al. 2015).

Dispersal may mask the importance of purely environmental control of local ecological communities (Palmer et al. 1996; Leibold et al. 2004; Brown et al. 2011; Winegardner et al. 2012). This is because very high or very low dispersal rates may interfere with species sorting, decoupling the otherwise strong relationships between biological communities and local environmental factors (Leibold et al. 2004; Ng et al. 2009; Brown and Swan 2010; Winegardner et al. 2012). For instance, in mass effects, very high dispersal from 'source' populations may produce a constant flow of migrants that guarantees the maintenance of populations in unsuitable or 'sink' localities (Pulliam 1988), thus interfering with local environmental control (Mouquet and Loreau 2003). On the other hand, species

77   may be absent from suitable localities owing to dispersal limitation (Heino et al. 2015a), also

78   contributing to low variation explained by environmental factors in multivariate models.

79   Multivariate models of community structure can typically explain only a small fraction (adj.

80    $R^2 < 50\%$, often varying between 0 and 20%) of community variation (Beisner et al. 2006;

81   Nabout et al. 2009; Alahuhta and Heino 2013; Soininen 2014; Heino et al. 2015b), which

82   may simply be due to unmeasured environmental factors, but also to our inability to

83   adequately account for dispersal in statistical models (Cottenie 2005; Leibold and Loeuille

84   2015; Soininen, 2016). An alternative view suggests that statistical models may also

85   overestimate the spatial component potentially related to dispersal, which may be due to

86   specifics of the spatial methods used (Gilbert and Bennett 2010; Smith and Lundholm 2010).

87   Therefore, refining the spatial methods and various proxies for dispersal should aid in taking

88   dispersal better into account in metacommunity ecology.

89   Understanding the utility of proxies for dispersal is also highly relevant for many

90   applied fields when the focus is on multiple species in freshwater ecosystems. These

91   ecosystems are all of high priority for bioassessment, restoration and conservation because

92   they comprise high levels of biodiversity (Dudgeon et al. 2006; Wiens 2015) and provide

93   crucial ecosystem services to humans (Vörösmarty et al. 2010; Garcia-Llorente at al. 2011;

94   Holland et al. 2011). At the same time, freshwater ecosystems are strongly threatened by

95   anthropogenic impacts such as eutrophication and habitat fragmentation (Dudgeon et al.

96   2006; Erős and Campbell Grant 2015). We emphasize that different types of freshwater

97   ecosystems (e.g. ponds, lakes, streams, rivers, springs) show different interactions among

98   dispersal, anthropogenic impacts and natural environmental factors. Owing to lower

99   connectivity, it may be that organisms in isolated freshwater ecosystems (e.g. ponds and

100   springs) are more severely impacted by the interactions of limited dispersal and

101   anthropogenic effects than those in more continuous ones (e.g. large rivers and large lake

102   systems). Similar interactions among dispersal, fragmentation and unexpected effects of

103   stressors may occur in all freshwater, marine and terrestrial ecosystems. Therefore, the use of

104   proxies for dispersal will be essential for applied research in all ecosystems. For example, our

105   typical reasoning is that the success of restoration projects (e.g. recovery from acidification)

106   may be delayed due to dispersal limitation because tolerant species may be absent from

107   ecosystems simply because they have not been able to reach the site. Similarly,

108   biomonitoring programs may be less effective in detecting impaired sites when dispersal from

109   pristine to impacted sites is high.

110   Our aim is to review current use of proxies for dispersal in freshwater ecosystems.

111   Individual sites in freshwater ecosystems are often inherently connected (Tonn and

112   Magnuson 1982; Palmer et al. 1996; Magnuson et al. 1998; Jackson et al. 2001; Olden et al.

113   2001; Grant et al. 2007; Altermatt 2013). It can be assumed that most of the dispersal of

114   obligate freshwater organisms, such as fish, is restricted to the network comprising running

115   and standing waters (Matthews 1998; Olden et al. 2001). However, for other freshwater

116   organisms, such as aquatic insects, dispersal within the network is not the only option, as

117   insect adults may show active and passive out-of-network dispersal (Malmqvist 2002; Smith

118   et al. 2009). Yet other groups of species, such as aquatic macrophytes, algae, mollusks and

119   crustaceans, may disperse passively through waterways, or their seeds, whole cells, fragments

120   or resting stages are carried by winds or animals for long distances (Kristiansen 1996; Bilton

121   et al. 2001; Bohonak and Jenkins 2003; Riis and Sand-Jensen 2006).

122   Variation in dispersal mode and ability among groups of organisms is also

123   exacerbated by the fact that even within a single group, dispersal distances vary greatly

124   among species. Rather than being intimidated by such high degrees of variation, we propose

125   that it actually provides a number of possibilities for basic and applied research. However,

126 better understanding of dispersal in diverse organisms inhabiting freshwater ecosystems is

127 dependent on the better use of existing proxies and the development of new approaches.

128 Here, we claim that while some traditional proxies are still useful, some proxies applied in

129 transport geography are promising tools for basic and applied metacommunity research.

130 Testing the utility of these proxies is, however, still in its infancy, and further case studies are

131 needed. One of the aims of this review is to provide motivation for such further studies.

132

133 **Past, present and future proxies for dispersal**

134

135 *The distance effect: "…near things are more related than distant things"*

136

137 According to Tobler's (1970) first law of geography, "Everything is related to everything

138 else, but near things are more related than distant things". Although this law is certainly

139 accurate in geography and ecology (Nekola and White 1999; Hubbell 2001; Soininen et al.

140 2007), it has an inherent emphasis on Euclidean distances between sites. Nature and

141 organisms are, however, more complex. What we define as "near" or "distant" should be

142 understood in the context of ecological, but not necessarily geographical, distances between

143 sites. Ecological distance takes into account structural (e.g. landscape features) and functional

144 (e.g. animal movements) aspects as related to dispersal (McRae 2006; Sutherland et al. 2015).

145 Hence, by necessity, those distances are much more complex than linear distances between

146 sites (Wang et al. 2009; Graves et al. 2014). Also, organisms differ from each other in their

147 dispersal ability (i.e. capacity to move long distances), although we can also state that all

148 organisms are different from other organisms, but phylogenetically closely-related organisms

149 are, on average, more similar than distantly-related organisms. Organisms thus also have

150 morphological (e.g. wing morphology in insects) and behavioural (e.g. tendency to fly long

151 distances) characteristics related to dispersal (Hoffsten 2004; Rundle et al. 2007), which are

152 typically phylogenetically conserved (Dijkstra et al. 2014). Below, we will consider pros and

153 cons of organismal, genetic, physical and transport geography (i.e. graph-based) proxies for

154 dispersal distances in a multi-species metacommunity context in freshwater systems (Table

155 1).

156

157 *Organismal-based proxies*

158

159 Organismal-based proxies for dispersal are important because they combine species traits and

160 the dispersal process. Typical organismal-based proxies for dispersal include separation of

161 species into more homogeneous groups according to body size (Jenkins et al. 2007; De Bie et

162 al. 2012; Datry et al. 2016a), wing size or wingspan (Hoffsten 2004; Sekar 2012), dispersal

163 mode (active vs passive, aquatic vs aerial) and dispersal ability (Thompson and Townsend

164 2006; Göthe et al. 2013a, 2013b; Grönroos et al. 2013; Heino 2013b; Cañedo-Argüelles et al.

165 2015; Heino et al. 2015a).

166   First, the use of body size divisions typically assumes that very small organisms are

167 easily carried long distances passively by water currents, wind or by animals, and that

168 increasing body size decreases the possibilities for passive long-distance dispersal (Fenchel

169 and Finlay 2004; Shurin et al. 2009). While this idea is partly supported by empirical findings

170 (De Bie et al. 2012; Padial et al. 2014; Datry et al. 2016a), some studies have also found little

171 support for it (Jenkins et al. 2007). Body size is also correlated with various life history and

172 ecological traits other than dispersal. For example, regarding freshwater ecosystems, body

173 size may correlate with predation pressure (e.g. Tolonen et al. 2003), number of generations

174 per year (e.g. Zeuss et al. 2017) and more, suggesting that using body size as a dispersal

175 proxy may be compromised by other ecologically-relevant factors.

176   Second, unless the dispersal mode is taken into account, body size is likely to be a

177 poor predictor of dispersal distances. It is likely that very small passively dispersing

178 organisms, such as bacteria, microfungi and microalgae, are able to disperse passively across

179 very long distances (Baas-Becking 1934; Kristiansen 1996). However, intermediate-sized and

180 actively dispersing organisms, such as many aquatic insects (except perhaps dragonflies),

181 may show rather limited dispersal distances (Finn et al. 2011). Also, large-sized actively

182 dispersing organisms, such as some diadromous fish or aquatic birds, may disperse (or rather

183 migrate) very long distances (Matthews 1998). Thus, body size should not be used alone

184 without considering dispersal mode.

185   Third, organismal classifications focusing on wing morphology, wing size or

186 wingspan might add considerably over using body size as a proxy for dispersal (see also

187 Harrison 1980). For example, studying aquatic insects Malmqvist (2002) and Hoffsten (2004)

188 found that larger-winged species had larger distributions that those with smaller wings,

189 suggesting that large wings might facilitate dispersal and lead to broader ranges. Malmqvist

190 (2000) also emphasised that wing size allows to identify poor dispersers among groups of

191 aquatic insects because it can be assumed that re-colonisation by poor flyers can be very

192 limited and slow after local extinction. This finding has implications for colonization-

193 extinction dynamics in metacommunities and consequent applications in environmental

194 research.

195   Given that various whole-organism based proxies have their limitations, researchers

196   should aim at finding a novel proxy or index for dispersal. Among aquatic invertebrates, for

197   example, a suitable index could consist of combined information from traits related to

198   dispersal mode, body size, life span, fecundity and more (e.g. Sarramajane et al. 2017).

199   Constructing such dispersal indices is possible using trait databases available in the literature

200   (Dolédec et al. 2006; Poff et al. 2006; Tomanova et al. 2007; Tachet et al. 2010) or in the

201   Internet (e.g. http://www.freshwaterecology.info/). However, it should be borne in mind that

202   such indices (i) should not be too complex to allow a widespread use, (ii) should account for

203   potential dispersal distances, and (iii) should be related to dispersal rates between sites (of

204   which fecundity and number of generations could be suitable indices). Such dispersal indices

205   should subsequently be tested using empirical datasets in metacommunity and environmental

206   assessment contexts.

207   An additional whole-organism based approach constitutes the use of stable isotopes to

208   mark individuals and measure dispersal (e.g. McNeale et al. 2005). While such an approach

209   may be feasible for a single species, it is increasingly difficult for large numbers of species

210   because recapturing rare species may be laborious or largely impossible. However, stable

211   isotopes can be used in estimating the dispersal distances of common freshwater species,

212   which could also inform about main patterns in metacommunity structuring.

213

214   *Molecular genetic proxies*

215

216   Another group of proxies are provided by advances in molecular biology. These include

217   population genetics (Hughes, 2007), DNA-barcoding (Cristescu 2014) and environmental

218 DNA (Bohmann et al. 2014). However, as these advances have been reviewed recently

219 (Manel et al. 2003; Manel and Holderegger 2013), we only mention briefly that they may

220 also be used as proxies for dispersal (Bohonak 1999; Wilcock et al. 2001; Hughes et al.

221 2009). These methods also have some drawbacks, such as "detecting" a species when it is not

222 actually present at a site in the environmental DNA approach (Bohmann et al. 2014). This is

223 probably because the 'signal' of a species' assumed presence may be carried long distances

224 from occupied sites to other sites where they will result in false presences.

225 Population genetic approaches used to infer dispersal are manifold, and they have

226 been available to researchers for decades (see reviews by Manel et al. 2003; Manel and

227 Holderegger 2013). They include approaches that inform about past and/or current

228 connections between local populations (Wilcock et al. 2001; Hughes et al. 2009). For

229 example, phylogeography tries to understand the geographic distribution of the different

230 genealogical lineages and can be used to infer past events (including long-term dispersal) by

231 considering the spatial genetic variation of current populations (e.g. Teacher et al. 2009).

232 More generally, genetic variation across populations (i.e. genetic structure) has been

233 traditionally used as an indirect measure of the current movement of individuals between

234 populations based on molecular markers and statistical methods (e.g. F_{ST}). There have been

235 some attempts to relate the genetic structure to the dispersal ability of species, showing that

236 sets of populations exhibiting high genetic diversity are those with low dispersal ability

237 (Bohonak 1999). Genetic structure can be, however, a biased proxy of dispersal because it

238 not only informs about gene flow among populations, but also about mutation, genetic drift,

239 adaptation by natural selection along environmental gradients and colonization history (i.e.

240 founder effects). Different theoretical and empirical models are currently being used to detect

241 these different processes (Orsini et al. 2013). Among them, isolation-by-distance (IBD)

242 models are commonly used to explain spatial genetic variation by gene flow and gradual

243   genetic drift. In this case, genetic similarity is reduced when geographical distance between

244   sites increases (Relethford 2004). However, IBD models are neutral models (Orsini et al.

245   2013) that do not consider changes in the environmental conditions in space and assume that

246   populations are in gene-flow-drift equilibrium, which is probably not the case of most natural

247   populations. In addition, disentangling the relative effects of gene flow from genetic drift is a

248   challenging task. Most direct methods used to measure gene flow require direct estimates of

249   dispersal, whereas indirect methods, which do not require dispersal information, still consider

250   equilibrium conditions. Gene flow is supposed to be more advantageous than traditional

251   dispersal proxies (e.g. mark-recapture methods) because it integrates multiple generations,

252   indicates successful establishment in the target population (in contrast to mark-recapture that

253   only assesses if individuals reached the target site) and can be applied across extensive

254   geographical areas (Bohonak 1999; Baguette et al. 2013). However, even if unbiased gene

255   flow estimates are obtained, they may not always fully represent dispersal because not all

256   dispersers survive and reproduce at a site (Bohonak and Jenkins 2003). Finally, recent

257   advances based on high throughput sequencing may lead to promising methods to measure

258   dispersal at the community level, as they may allow better quantification of genetic structure

259   and its underlying causes (e.g. Tesson and Edelaar 2013).

260

261   *Graph-based proxies*

262

263   Modelling is a prerequisite to examine the possible effects of using different dispersal proxies

264   in ecological research (Rouquette et al. 2013; Weinstein et al. 2014). One of the most

265   promising approaches is to examine the studied system as a graph, a set of nodes and links, in

266 which nodes represent the elements of the system (e.g. habitat patches, individuals,

267 populations or communities) and links specify the connectivity relationships between the

268 elements (Calabrese and Fagan 2004; Urban et al. 2009). In graph-based analyses, spatially

269 explicit data derived from geographic information systems (GIS) can be combined with

270 information on the dispersal of organisms (Calabrese and Fagan 2004). Different distance

271 classes among the nodes can be set up and depicted by adding different weights to the links

272 as a proxy for indicating habitat suitability for the dispersing organisms (e.g. flow and

273 riverbed characteristics for benthic insects) or barriers (e.g. dams or waterfalls for fish).

274 Directed links can refine the graph model representing the importance of upstream vs

275 downstream or watercourse vs overland dispersal (Galpern et al. 2011; Erős et al. 2012).

276 Potential connections between habitat patches (nodes) can be further refined by incorporating

277 information on the dispersal ability of the focal species. For instance, if the distance between

278 a given pair of patches is larger than a given threshold (here, dispersal distance for a species),

279 the patches may be considered unconnected.

280   Overall, graphs are useful for quantifying the physical relationships among the

281 landscape elements (i.e. structural connectivity; e.g. Saura and Rubio 2010) and how this

282 topological structure affects the movement of organisms across the landscape (i.e. potential

283 functional connectivity; e.g. Vasas et al. 2009). Graphs can thus help understanding the role

284 of dispersal in a diverse array of ecological systems in a flexible, iterative and exploratory

285 manner with relatively little data requirements (Urban and Keitt 2001; Calabrese and Fagan

286 2004; Dale and Fortin 2010).

287   As explained above, the construction of a graph model requires the determination of

288 links (connections) and their weights. In ecological research, many different

289 conceptualizations of physical distance can be used for this purpose, such as Euclidean,

290   network, flow and topographical distances (Olden et al. 2001; Beisner et al. 2006; Jacobson

291   and Peres-Neto 2010; Landeiro et al. 2011; 2012; Maloney and Munguia 2011; Liu et al.

292   2013; Silva and Hernández 2015; Cañedo-Argüelles et al. 2015; Kärnä et al. 2015; Datry et

293   al. 2016a). Euclidean distance is simply the shortest distance between two sites (Fig. 1). In

294   contrast, network distance takes into account riverine or other ecological corridors and thus

295   measures the shortest route from one site to another via corridors. However, according to

296   Peterson, Theobald and Ver Hoef (2007), "the physical characteristics of streams, such as

297   network configuration, connectivity, flow direction, and position within the network, demand

298   more functional, process-based measures". These authors made a useful distinction between

299   symmetrical distance (i.e. Euclidean and watercourse distance) and asymmetric distance

300   classes, which include upstream and downstream asymmetric flow distance (Peterson et al.

301   2007). This is because upstream dispersal is more difficult than downstream dispersal from

302   one site to another, at least for obligatory aquatic organisms. Finally, topographical distance

303   is built on the notion that altitudinal variation and slope may direct the dispersal of terrestrial

304   organisms, whereby they may choose optimal routes by avoiding steep upward slopes (Fig.

305   1).

306   Besides the traditional measures of between-site physical distances, cost distance is an

307   alternative family of distance metrics. Cost distance is calculated over a cost surface,

308   representing the resistance to an organism's movement. It can be metaphorically called "as

309   the fox runs" (Kärnä et al. 2015), as a wise animal like fox may choose a path of least

310   resistance in the landscape. Cost distance can be measured either as a least-cost (optimal)

311   path, or as a range of cumulative costs of landscape resistance between sites. Environmental

312   variables used to produce cost surfaces typically include land use, human constructions and

313   topography (Zeller et al. 2012). This technique has been mostly used to model the movement

314   and dispersal of large land mammal species of conservation concern (Larkin et al. 2004;

315 LaRue and Nilsen 2008), but it may also be relevant for the organisms living in freshwater

316 ecosystems (Kärnä et al. 2015).

317   Previous studies using cost distances have mainly employed categorical variables and

318 have not always taken into account variation in topography. In addition, various other

319 physical structures can be used as costs (Fig. 1). For example, the directional effect caused by

320 prevailing wind or flow conditions could be incorporated as part of cost distances (Horvath et

321 al. 2016). Additional cost can also consist of waterfalls, dams and other physical barriers for

322 fish (Olden et al. 2001; Pelicice and Agostinho 2008; Filipe et al. 2013) or inhospitable routes

323 through the matrix preventing or reducing dispersal, including pools, ponds and lakes for

324 riffle-dwelling species (Erős and Campbell Grant 2015). The same applies for deforested

325 riparian areas for terrestrial adults of freshwater species (Smith et al. 2009; Erős and

326 Campbell Grant 2015).

327   Although cost distances, least-cost path modelling and other approaches related to

328 graph-based modelling have been widely applied in ecology (e.g. Pinto and Keitt 2009), the

329 studies to date have mostly considered one species at a time (see review by Sawyer et al.

330 2011). A problem in the extension of this approach to sets of species is that their dispersal

331 routes and environmental responses likely differ. For instance, it is possible to assign costs to

332 links based on habitat suitability, although the latter likely differ for different species. A first

333 approach would be to split the species in functional sets that respond similarly to

334 environmental conditions and distance between sites. The straightforward extension of this

335 process would be the modelling of each species separately, each one with their costs, and

336 then combine all graphs in a more realistic description of communities. This approach,

337 however, should not be practical for many groups of organisms as we lack information on

338 their natural history.

339   The application of graph-based models is still limited in basic and applied

340   metacommunity research (Borthagaray et al. 2015; Layeghifard et al. 2015), and most

341   applications to date have been in the terrestrial realm, whereas the use of spatially explicit

342   graph-based methods in freshwater ecology has lagged far behind (Erős et al. 2012).

343   However, since graph-based modelling is widely used in many disciplines, proxies developed

344   in other fields can also be adopted in ecological research. One such field is transport

345   geography, encompassing various measures of spatial accessibility and interaction, as well as

346   methods for path or route selection in space. Next, we will consider how proxies utilized

347   previously in transport geography might allow modelling dispersal effects on local

348   communities when other approaches are not feasible for studying multiple species at the same

349   time. We suggest that some of these models can also be integrated in metacommunity

350   research in freshwater systems.

351   In traditional transport geography, researchers have tried to explain complex human

352   travel patterns by using spatial and spatio-temporal models (Black 2003). The modelling of

353   human travel patterns relies, to a large extent, on the notion of accessibility (Table 2, Fig. 2).

354   Accessibility can be defined as "the potential for reaching spatially distributed opportunities",

355   and its quantification typically includes the physical distance or cost of travel, as well as the

356   quality and quantity of opportunities that humans want to reach (Páez et al. 2012). In the

357   ecological context, the quality and quantity of opportunities might translate into habitat

358   quality in terms of water chemistry (e.g. pH or nutrients) and quantity of resources (e.g.

359   abundance of prey for predators). These qualities and quantities should be contrasted with the

360   ease to access them, i.e., ecologically meaningful distances between source and destination

361   localities in the landscape.

362   A number of measures have been devised for describing transport accessibility. These

363 can be broadly divided into connectivity, accessibility of nearest object, cumulated

364 opportunities, gravity and utility measures (Kwan 1998; Rietveld and Bruinsma 1998; Páez et

365 al. 2012). Connectivity measures describe the number or rate of connections for a specific

366 site, such as interconnectivity of a location to other locations within varying topology of a

367 road network (Xie and Levinson 2007). Accessibility of nearest object is measured as least-

368 cost path, for example, by applying street network travel distances to measuring the reach of

369 service facilities (Smoyer-Tomic et al. 2006). Cumulated opportunities measure the number

370 of opportunities (e.g. "available" sites for a species in ecological terms) reached within a

371 certain travel cost, which can be applied to indicate amount of reachable services in an urban

372 environment (Páez et al. 2012). While these measures mostly deal with the presence of a

373 connection between any two sites or the distance separating them, the purpose of gravity

374 measures is to express spatial interactions between sites. Drawing directly on the principles of

375 the law of gravity in physics, gravity measures assume that the attraction of a site increases

376 with size (or any other attribute) and declines with distance, travel time or cost. This is easily

377 translated into dispersal of species between localities in a metacommunity, whereby some

378 sites attract more individuals and species than others given the same dispersal distances, time

379 or cost. Also, for example, potential of human social interaction can be estimated within

380 urban and regional structures by applying daily time and travel constraints of people in

381 relation to residential, work and other activities (Farber et al. 2013). In freshwater systems,

382 this approach can include evaluation of species dispersal with different dispersal abilities

383 within a metacommunity and can be incorporated into the gravity models. Utility measures

384 are similar to gravity measures, but they are based on individual-related choices aiming to

385 maximize utility in the selection of the destination (Geurs and van Wee 2004). This can be

386   seen as a kind of habitat selection by individual organisms (e.g. oviposition by female insects

387   and nest-site selection by birds), which in turn affects local community structure.

388   While transport geography is an interesting source of proxies to be conflated with

389   ecological approaches, there is some overlap in the graph-based proxies used in transport

390   geography and metacommunity research. Such overlap is not always easy to detect since

391   vocabulary is not fully consistent across disciplines. Nevertheless, although some of the

392   proxies and terms have been used in metacommunity ecology before, transport geography

393   provides explicit formulas for further ecological applications and defines complex issues in

394   general terms.

395   There is one potential limitation with the use of physical and transport geography

396   proxies: the lack of suitable landscape-level environmental data in some regions. However,

397   our premise is that when environmental data are needed, they could be acquired from existing

398   databases or using modern geospatial data compilation techniques. These include land use

399   and land cover information using vast sets of airborne or spaceborne remote sensing sensors

400   and topographic information (including delineation of stream networks) from high-resolution

401   digital elevation models. Naturally, micro-scale explorations would require more accurate

402   spatial data than available in most of the global data banks. However, similar remote sensing-

403   based acquisition techniques (e.g. terrestrial hyperspectral and LiDAR imaging) could be

404   applied in fine-scale investigations using the physical and transport geography proxies.

405   Another caveat in applying all physical and transport geography proxies is that

406   although they describe 'physical connectivity' between sites, they do not necessarily translate

407   easily into 'biological connectivity'. Hence, researchers should keep this limitation in mind

408   and try combining organismal proxies with physical connectivity among sites. One approach

409   is also to take into account biological similarity between sites, with the assumption that

410   biological dissimilarity provides information about the biological connectivity between sites

411   (Layeghifard et al. 2015; Monteiro et al. 2017; see below).

412

413   **Use of different proxies for dispersal in the literature**

414

415   In order to roughly estimate the frequency of usage of different proxies for dispersal, we

416   conducted a literature search using the Web of Science database (from 2004 to August 26,

417   2016) and the terms (Dispers* AND metacommunity*), in the field TOPIC. These terms

418   were combined, also in field TOPIC and using the Boolean operator "AND", with keywords

419   related to the different proxies evaluated in this review (Table 3). Thus far, terms related to

420   organismal-based proxies were the most frequent, followed by physical distance-based

421   proxies. However, we did not find articles using terms that would indicate the use of transport

422   geography proxies in metacommunity ecology.

423   In studies using organismal-based proxies, a possible analytical approach consists of

424   the creation of different matrices comprising taxa with different (yet typically inferred)

425   dispersal abilities. These matrices may then be analyzed using variation partitioning methods

426   (see examples below). The frequency of usage of spatial eigenfunction analysis and simple

427   polynomials of geographic coordinates (i.e. distance-based proxies) was likely

428   underestimated in our search. For example, Soininen (2014; 2016) found a total of 322 data

429   sets, which were analyzed with variation partitioning methods (most of which were from

430   lakes and streams). However, many data points in Soininen's (2014; 2016) studies originated

431   from one paper (Cottenie 2005), which was also counted as a single paper in our literature

432   searches. We thus believe that our keyword analysis confidently reveals that use of more

433   elaborate proxies for dispersal (considering, for instance, transport geography proxies) are

434   less frequent than simple and possibly too simplistic proxies. In summary, our keyword

435   analysis indicates the need for further comparative studies to better take dispersal into

436   account in metacommunity studies.

437

438   **Statistical approaches to model dispersal influences on biological communities**

439

440   There are many spatial statistical approaches to study species distributions and community

441   structure that incorporate physical distance proxies, including the Mantel test (Mantel 1967),

442   eigenfunction spatial analysis (Borcard and Legendre 2002) and related methods (for a

443   comprehensive review, see Legendre and Legendre 2012). For example, the flexibility and

444   usefulness of eigenfunction spatial analysis and other similar methods in spatial modelling

445   have been stressed elsewhere (Griffith and Peres-Neto 2006; Dray et al. 2006; Dray et al.

446   2012), and we briefly emphasize that they deserve their place in community ecologists'

447   toolbox. Eigenfunction spatial analyses allow one to use different types of distance (e.g.

448   overland, watercourse and flow distance), geographic connectivity matrices and information

449   about directional spatial processes (Blanchet et al. 2008; 2011; Landeiro et al. 2011; Göthe et

450   al. 2013a; Grönroos et al. 2013) as inputs to compute eigenvectors (i.e. spatial predictors for

451   univariate regression or multivariate constrained ordination analyses). This offers important

452   flexibility to model complex spatial phenomena (Griffith and Peres-Neto 2006), such as

453   variation of community structure (Dray et al. 2012). However, it has also been suggested that

454   the explanatory variables derived from spatial eigenfunction analysis may overestimate

455   spatial structure and the potential effects of dispersal on biological communities (Bennett and

456   Gilbert 2010; Smith and Lundholm 2010). Also, spatial patterns in metacommunity structure

457   may have emerged due to the effects of environmental variables, which are themselves

458   spatially patterned and, more importantly considering the scope of this review, due to

459   dispersal processes. In short, after controlling for the effects of environmental variables (e.g.

460   using variance partitioning; see Peres-Neto et al. 2006; Legendre and Legendre 2012), the

461   spatial variables can be used to infer the relative role of dispersal processes. In studies of

462   metacommunity structure, this inference is valid only if one assumes that no relevant

463   environmental variables have been overlooked and that the effects of biotic interactions on

464   the spatial patterns of community structure are negligible (Peres-Neto and Legendre 2010;

465   Vellend et al. 2014).

466   Layeghifard et al. (2015) suggested weighting a spatial matrix (be it overland or not)

467   by a dissimilarity matrix derived from a community data matrix. Accordingly, connectivity

468   between a focal site and two other equally-distant sites will not be identical, but are

469   dependent on biological dissimilarity. The more similar the focal site is to one of the sites, the

470   higher is their assumed connectivity (Layeghifard et al. 2015). It is probably possible to

471   modify these methods to accompany more complex relationships between sites in space. For

472   instance, it could be possible to use the suite of distance classes referred to earlier in this

473   review (Table 1). Also, if a gravity model of connectivity is hypothesized to represent

474   dispersal, for instance, from headwaters to mainstreams and the latter accumulates more

475   species, a suitable dissimilarity index may be one that measures species turnover only and not

476   species richness differences (Lennon et al. 2001; Baselga 2010; Legendre 2014).

477

478   *Combining organismal and physical distance proxies in the same modelling study*

479

480 A few studies have considered simultaneously organismal and physical distance proxies. For

481 example, Kärnä (2014) and Kärnä et al. (2015) studied a stream insect metacommunity in a

482 subarctic drainage basin in Finland and examined how physical distance proxies affect

483 different groups of insects defined by body size and dispersal mode. As physical distances,

484 they used (1) overland, (2) watercourse, (3) least-cost path (i.e. optimal routes between sites

485 in landscape) and (4) cumulative cost (i.e. cumulative landscape resistance between sites

486 along the optimal route) distances (Kärnä 2014; Kärnä et al. 2015). They calculated Mantel

487 correlations and partial Mantel correlations between Bray-Curtis biological community

488 dissimilarities and environmental distances or each of the four types of physical distances. In

489 these data, environmental and spatial distances were not strongly correlated, and the results of

490 partial Mantel test were hence very similar to the Mantel tests shown here (Fig. 3). Kärnä et

491 al. (2015) found that environmental distances between sites were most strongly correlated

492 with all biological dissimilarity matrices, as has been shown previously for stream

493 metacommunities (Heino et al. 2015b). However, different types of physical distances were

494 also often significant for different subsets of stream insect assemblages, even when

495 environmental effects were controlled for. A similar pattern has also been found in streams of

496 other climatic zones (Cañedo-Argüelles et al. 2015; Datry et al. 2016b). What is more

497 important is that the more complex cumulative cost distances were either equally good or

498 sometimes even outperformed the typically-used overland and watercourse distances in

499 accounting for variation in biological community dissimilarities between sites, although this

500 varied between different subsets of stream insect assemblages (Kärnä et al. 2015).

501 The approaches using cost distance-based modelling could also be strengthened by

502 the use transport geography proxies. For example, Cañedo-Argüelles et al. (2015), Kärnä et

503 al. (2015) and Datry et al. (2016b) could also have used measures related to 'cumulative

504 opportunities', 'population attraction and competition between destinations' or 'gravity'

505 measures (Table 2) when examining metacommunity organization in streams. For instance, in

506 terms of gravity, nodes in the mainstem of a basin may support large population sizes and,

507 thus, provide much more migrants than small tributaries. We are currently striving to begin

508 applying these measures in our studies of stream metacommunity organization and

509 environmental assessment, and also urge other researchers to focus on these and other

510 relevant proxies in various ecosystem types.

511

512 **Applications of proxies for dispersal**

513

514 *Applied research benefitting from use of dispersal proxies*

515

516 While the importance of dispersal is well appreciated in fundamental ecology, applied

517 research has lagged behind in integrating dispersal effects on biological communities

518 (Bengtsson 2010; Heino 2013a). For example, current bioassessment approaches infer effects

519 of environmental changes using the responses of bioindicators to environmental factors

520 (Hawkins et al. 2000a; Friberg et al. 2011). However, sole reliance on local environmental

521 control (i.e. species sorting) may be misleading (Heino 2013a; Friberg 2014). In species

522 sorting, adequate dispersal guarantees that all species are available at a locale to be filtered by

523 local environmental factors (Leibold et al. 2004; Holyoak et al. 2005). However, high

524 dispersal rates from unpolluted to polluted sites as in source-sink dynamics (Pulliam 1988)

525 may decrease our ability to detect environmental change through the use of bioindicators.

526 Some species indicative of pristine conditions may occur at the polluted site owing to high

527 dispersal rates, even if that site is not favourable for them in the long term, thus masking the

528 influence of anthropogenic changes on local biota. In contrast, owing to dispersal limitation,

529 some pristine reference sites may also lack species that would otherwise occur there, thus

530 affecting bioassessment results. Hence, we support the idea derived from simulation analyses

531 (Siqueira et al. 2014) that potential dispersal effects should be directly integrated in aquatic

532 bioassessment studies (Heino 2013a; Alahuhta and Aroviita 2016).

533 Restoration ecology is another field that might benefit from greater insights about

534 dispersal. Restored sites may lack many species simply because potential donor communities

535 were all impacted by pollution or habitat degradation in a region, and colonization will thus

536 be slow and initially composed mostly of dispersal-prone species (Bond and Lake 2003).

537 Another possibility in this context relates to delayed recolonization of ecosystems that are

538 recovering from anthropogenic stressors due to dispersal limitation (Blakely et al. 2006; Gray

539 and Arnott 2011; 2012). Restoration ecology should thus take into account ecological

540 corridors for dispersal, which might facilitate the recolonization of previously denuded or

541 restored sites (Tonkin et al. 2014). The efficiency of ecological corridors is also dependent on

542 dispersal ability and the spatial configuration of these corridors in the landscape (Joly et al.

543 2001). Hence, rather than restoring only local sites, restoration of connectivity is also a

544 prerequisite for successful local restoration outcomes (see also McRae et al. 2012).

545 Conservation planning is a third field of applied research that should take dispersal

546 directly into consideration. This is because dispersal within and between protected areas

547 should be guaranteed (Jaeger et al. 2014; Barton et al. 2015a), and the network of protected

548 areas should be planned such that they can act as stepping-stones to allow organisms to

549   respond to environmental change (Fahrig and Merriam 1994; Margules and Pressey 2000;

550   Lechner et al. 2015). However, conservation planning is also challenged by the vast numbers

551   of species that should be monitored over broad metacommunities (e.g. Heino 2013a) and

552   macrosystems levels (e.g. Heffernan et al. 2014), which is also exacerbated by the difficulties

553   to measure dispersal over broad spatial scales. As a "science of crisis" (Soulé 1985),

554   conservation biology cannot wait for the development and application of sophisticated, time-

555   consuming and expensive methods of measuring dispersal directly for hundreds to thousands

556   of species and, at least in the short-term, the best we can do is to rely on proxies for dispersal.

557

558   *The importance of integrating dispersal in predictive models of global change*

559

560   Dispersal should be directly considered in predictive models in ecological research. Ecology

561   has become increasingly predictive, most likely due to the need to forecast the effects of the

562   ongoing global change (Evans et al. 2012; Petchey et al. 2015). Over the past decades,

563   several models have been designed to predict how populations, communities or ecosystems

564   will respond to ecological changes in time and space. Predictive models have been used to

565   forecast distributions of species based on their climatic niches using Species Distribution

566   Models (SDMs; Guisan and Zimmerman 2000; Chu et al. 2005) and, for example, to assess

567   ecological status by comparing the observed community in a water body with the one

568   expected under reference conditions (Hawkins et al. 2000a; Clarke et al. 2003). However,

569   despite the wide use of both approaches, predictions can be biased if dispersal is not

570   considered. Suitable habitats can be available for a species, but its real occurrence will

571   ultimately depend on its ability to reach the site.

572   SDMs have been criticized because most of them only consider niche characteristics

573 of species and neglect biotic interactions (Wisz et al. 2013), evolutionary changes (Thuiller et

574 al. 2013) or dispersal processes. Several attempts have been made to incorporate dispersal

575 into SDMs (e.g. Araújo et al. 2006). This is usually done by considering two extreme degrees

576 of dispersal limitation (e.g. no dispersal vs unlimited dispersal) or intermediate situations

577 using probabilistic methods when data on the dispersal abilities of the species are available

578 (Barbet-Massin et al. 2012). Some modelling endeavours have also acknowledged the need to

579 consider barriers to dispersal (e.g. dams) to improve model accuracy (Filipe et al. 2013).

580 Information on current spatial connectivity across populations based on genetic approaches

581 could also be used in SDMs to improve model accuracy (Duckett et al. 2013).

582   A possibility to construct models encompassing responses of multiple species at the

583 same time include the River InVertebrate Prediction And Classification System (RIVPACS),

584 first applied in riverine ecosystems (Wright et al. 2000; Clarke et al. 2003), but which can

585 also be applied in other freshwater, marine and terrestrial ecosystems. There have been no

586 empirical attempts to include dispersal in the practical applications of RIVPACS-type

587 models, but simulations have shown the potential importance of dispersal for bioassessment

588 (Siqueira et al. 2014). At best, some of these types of models consider spatial coordinates (i.e.

589 latitude and longitude) as model predictors, but are usually based on assumptions about the

590 niche characteristics of species (i.e. environmental filtering; Friberg et al. 2011). The

591 importance of using dispersal proxies as predictor variables in bioassessment models is of

592 particular significance in the context of metacommunities (Heino 2013a). This is because the

593 spatial connectivity of sites and the dispersal abilities of the species may hinder the ability of

594 models to detect an impact (Alahuhta and Aroviita 2016). This is especially relevant in less

595 impacted and highly isolated sites (Siqueira et al. 2014). In addition, these sites (e.g. isolated

596 headwater streams) usually host species with narrow ecological niches and distribution

597 ranges, which can also have limited dispersal abilities (Finn et al. 2011). Incorporating

598 organismal and physical distance proxies for dispersal in the metacommunity-level

599 bioassessment could help to increase the accuracy of these models and thus the management

600 of constituent freshwater ecosystems.

601

602 **Questions for further freshwater research**

603

604 The importance of dispersal proxies can be revealed by a number of questions that should be

605 considered in basic and applied freshwater ecology. Although these ideas are somewhat

606 speculative at present, they may provide useful roadmaps for further studies on dispersal

607 proxies in bioassessment, restoration and conservation biology.

608

609 *How important are stepping-stones for dispersal and how they can be recognized?*

610

611 Ecological stepping-stones can be defined as sites or areas that help species to disperse from

612 a site to other suitable sites across inhospitable landscapes. Stepping-stones can be expected

613 to be very important for species dispersal (Saura et al. 2014; Barton et al. 2015a), but their

614 recognition may be difficult. If we can recognize such sites in landscapes by applying

615 organismal and physical distance proxies in combination or based on transport geography

616 measures, there are better possibilities to plan the conservation of metapopulations and

617 metacommunities. For instance, we should be able to recognize sites having high accessibility

618   for multiple species and subsequently plan a network of such sites across a broader

619   landscape.

620   Graph-based modelling can also help if field-based measures fail to highlight the

621   importance of stepping-stones for dispersal (Galpern et al. 2011). For example, network

622   analyses can reveal how connectivity relationships change in the landscape if stepping-stones

623   are deleted from the network of habitat patches. The importance of stepping-stones and other

624   patches can be prioritized using different indices (e.g. Rayfield et al. 2011), which quantify

625   the importance of the focal habitat to maintaining connectivity between the patches (e.g.

626   Pereira et al. 2011). Their more widespread application is warranted, especially for network-

627   like stream systems, where habitat patches and their boundaries may be not so easily

628   recognized (Erős and Campbell Grant 2015).

629

630   *Are very low or very high dispersal rates affecting bioassessment?*

631

632   Dispersal limitation may lead to a situation where not all species are available in reference

633   sites (Pärtel et al. 2011; Cornell and Harrison 2014). A traditional approach has been to use a

634   regional stratification to focus on smaller geographical areas, which could ensure that all

635   species are able to reach all sites within a relatively small region (e.g. Hawkins et al. 2000b)

636   and persist on them (e.g. Cornell and Harrison 2014). This should facilitate the detection of

637   species sorting mechanisms and help define reference conditions. However, temporary local

638   extinctions at suitable sites may not always be counterbalanced by immediate colonization if

639   other suitable sites are located far away from the focal site even within a small region (Heino,

640   2013a) and/or if species have weak dispersal ability. In this case, we may classify sites in the

641   wrong reference site group (or as impacted) if some species that should occur according to

642   environmental conditions are absent from a site. It might be possible to adjust our predictive

643   modelling efforts by using physical distance proxies (see Table 2), which might lead to a

644   better prediction success. Alternatively, we could focus on a subset of good dispersers in our

645   dataset, which should show minor effects of dispersal limitation, or focus on resident species

646   (i.e. those species that do not show strong propensity for migration), which may show

647   stronger associations with environmental gradients than entire assemblages (Bried et al.

648   2015).

649   The mass effects perspective in metacommunity ecology (Mouquet and Loreau 2003)

650   suggests that high dispersal between localities may homogenize, at least to some degree,

651   community structure in adjacent sites. On the other hand, some species may be absent from a

652   site owing to not having been able to reach the site yet due to low dispersal rates or small

653   source population size (Leibold et al. 2004). Either way, it may be difficult to assess if

654   anthropogenic stressors have impacted a site, as extra species may be present or some

655   expected species are missing (Siqueira et al. 2014). This limits our bioassessment by not

656   detecting change correctly. Using information about the species composition of nearby sites

657   might help us to decipher if either high or limited dispersal is affecting our bioassessment and

658   restoration endeavours (Tonkin et al. 2014). These could be quantified by taking

659   simultaneously into account a site's accessibility and relative quality in the landscape, and

660   how it attracts dispersers from the surrounding metacommunity. For instance, the measures

661   from transport geography described above (e.g., gravity or utility measures, Table 2) could be

662   used to show that the lower than expected biological differences between reference and

663   impacted sites are due to their strong spatial connectivity and species exchange in terms of

664   high dispersal.

665

666   *Will species reach all potential future habitats in the face of global environmental changes?*

667

668   Even though environmental conditions change, not all species may be able to track those

669   changes (Heino et al. 2009; Poff et al. 2012). Poor dispersers or those with small source

670   populations may not be able to disperse to suitable new habitats in other areas, at least if not

671   assisted by humans. If such poorly-dispersing species can be identified based on their

672   organismal traits, there are more possibilities for success (Bhowmik and Schäfer 2015). Also,

673   if their actual dispersal routes can be approximated using physical distance proxies, the

674   success of the species for founding self-maintaining metapopulations and metacommunities

675   may be better in the face of global change. For example, global change may lead to increase

676   in temporal fragmentation of river networks, i.e., the degree of intermittency, which should

677   affect the connectivity between stream sites (Datry et al. 2014). Improving our ability to

678   predict changes in stream communities using distance-based proxies accounting for this

679   fragmentation will improve our capacity to assess, estimate and mitigate the effects of global

680   changes on intermittent streams (Datry et al. 2016c).

681

682   *How can the dispersal of invasive species be predicted using proxies?*

683

684   Knowing the dispersal ability of an invasive species (i.e. an organismal-based proxy) helps to

685   predict its rate and potential to spread over large areas. Furthermore, knowing how landscape

686   resistance (i.e. a physical distance proxy) may hinder its spread may have obvious benefits

687   for predicting or preventing its dispersal. In this case, applications of the gravity or utility

688   measures originated from the transport geography might also be useful, as the accessibility

689   and attraction of sites for invasive species could be revealed using suitable proxy measures.

690   Hypothetically, some widely recognized man-made structures that impair dispersal of native

691   species such as dams (Winemiller et al. 2016) might, at the same time, boost the spread of

692   invasive species (Havel et al. 2005).

693

694 *How can we best detect and restore dispersal routes between near-pristine sites?*

695

696 Local populations and communities at near-pristine or pristine sites need to be connected by

697 gene and organism flows in order to remain viable (Fahrig 2003). Conservation and

698 restoration efforts should also target the maintenance of the most efficient dispersal routes to

699 and from these pristine sites, although identifying these routes remains a challenge. Dispersal

700 proxies could offer an efficient tool to identify these routes for all types of species, from poor

701 to strong dispersers, and therefore provide insights to ecosystem managers for designing

702 restoration and conservation projects (Tonkin et al. 2014; Cañedo-Arguelles et al. 2015;

703 Kärnä et al. 2015; Datry et al. 2016a).

704

705 *Can restoration measures fail due to lack of dispersers from neighbouring sites?*

706

707 Restoration practices may not attain the planned objectives, or only attain them after long

708 periods, if species are not able to colonize restored habitats in a strongly human-impacted

709 landscape (Bond and Lake 2003; Tonkin et al. 2014; Barton et al. 2015b). Accordingly,

710 restoration measures should be initially focused on sites connected to non-impacted source

711 habitats or be planned to encompass entire landscapes or catchments that include some source

712 localities (Bond and Lake 2003). Also, restoration practices should be coupled with the

713 restoration of adjacent ecosystems to enhance suitable habitat corridors for dispersing species

714 (Smith et al. 2009). Identifying such habitat corridors using the physical-based or transport

715 geography proxies might be useful in this context.

716

Where to go from here?

718

719   Barton et al. (2015a) suggested that ecologists have made little effort to validate the use of

720   proxies in ecology. For example, from a bioassessment perspective, the generally assumed

721   conceptual model (e.g. environmental change $\rightarrow$ local community structure) suggests that a

722   change in the environment (e.g. pollution) causes a change in local community structure (e.g.

723   changes in species composition and relative abundances of species). However, dispersal

724   disrupts this basic model and, to tease apart this effect, one needs a proxy for dispersal, which

725   would function as a covariate (e.g. environmental change $\rightarrow$ local community structure $\leftarrow$

726   proxy for dispersal). This covariate should, for instance, take mass effects or dispersal

727   limitation into account. As shown in this essay, there are a number of ways to express the

728   level of spatial relationships between sites and the best way may well be case-specific,

729   depending on a study system, regional environmental conditions, between-site connectivity

730   and characteristics of biotas. Thus, we propose that freshwater ecologists should evaluate and

731   quantify the relationship between the biological dataset at hand and different proxies for

732   dispersal (e.g. organismal-based dispersal traits, Euclidean, watercourse, least-cost path

733   distances, and more). However, for the sake of generality, testing the predictability of

734   different proxies in different regions, with different groups of organisms and in different

735   points in time is also warranted (Barton et al. 2015a). In this context, a promising direction

736   for future work would be to utilize the data from previous studies on bioassessment,

737   restoration, conservation biology and community ecology, with the objective of quantifying

738   the relative importance of different proxies for dispersal using a meta-analytical approach. A

739   second objective would be, after knowing which proxy to use, how to integrate a proxy into

740 practical management of biodiversity. This is an open call for researchers interested in such

741 proxies for dispersal.

742

743 **Conclusions**

744

745 Dispersal proxies include traditional physical distances used in ecological research, such as

746 Euclidean distances, network distances, and various organismal-based proxies, such as body

747 size, dispersal mode and dispersal ability. More recent approaches include graph-based

748 methods, which show considerable promise for freshwater research. Future studies should

749 also consider applying methods developed in other disciplines, such as transport geography.

750 Application of these proxies should not be limited to fundamental ecological research, but

751 they should also be widely considered in applied fields, such as bioassessment, conservation

752 and restoration ecology. As dispersal is an essential element affecting species distributions, it

753 should be communicated to environmental managers and policy makers responsible for

754 practical conservation, management and assessment issues (Barton et al. 2015b). Hence,

755 while dispersal proxies should be efficient enough in capturing dispersal as a phenomenon,

756 they should also be simple enough to be useful in practical solutions. We propose that

757 organismal, physical and transport geography proxies for dispersal should be widely

758 considered as tools guiding environmental management and decision making.

759

760 **Acknowledgments**

761

33

770

References

772

773 Alahuhta, J., and Aroviita, J. 2016. Quantifying the relative importance of natural variables,

774   human disturbance and spatial processes in ecological status indicators of boreal

775   lakes. Ecol. Ind. **63**: 240-248.

776 Alahuhta, J., and Heino, J. 2013. Spatial extent, regional specificity and metacommunity

777   structuring in lake macrophytes. J. Biogeogr. **40**: 1572-1582.

778 Altermatt, F. 2013. Diversity in riverine metacommunities: a network perspective. Aquat.

779   Ecol. **47**: 365-377.

780 Araújo, M. B., Thuiller, W., and Pearson, R. G. 2006. Climate warming and the decline of

781   amphibians and reptiles in Europe. J. Biogeogr. **33:** 1712-1728.

782 Baas-Becking, L. G. M. 1934. Geobiologie of inleiding tot de milieukunde. The Hague, the

783   Netherlands: W.P. Van Stockum and Zoon.

784 Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., and Turlure, C. 2013. Individual

785   dispersal, landscape connectivity and ecological networks. Biol. Rev. **88**: 310-326.

786 Barbet-Massin, M., Thuiller, W. and Jiguet, F. 2012. The fate of European breeding birds

787   under climate, land-use and dispersal scenarios. Glob. Chang. Biol. **18**: 881-890.

788 Barton, P. S., Lentini, P. E., Alacs, E., Bau, S., Buckley, Y. M., Burns, E. L., Driscoll, D. A.,

789   Guja, L. K., Kujala, H., Lahoz-Monfort, J. J., Mortelliti, A., Nathan, R., Rowe, R.,

790   and Smith, A. L. 2015a. Guidelines for using movement science to inform

791   biodiversity policy. Env. Manag. **56**: 791-801.

792 Barton, P. S., Pierson, J. C., Westgate, M. J., Lane, P. W., and Lindenmayer, D. B. 2015b.

793   Learning from clinical medicine to improve the use of surrogates in ecology. Oikos

794   **124**: 391–398.

795 Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity.

796   Glob. Ecol. Biogeogr. **19**: 134-143.

797 Beisner, B. E., Peres-Neto, P. R., Lindstrom, E., Barnett, A., and Longhi, M. L. 2006. The

798   role of dispersal in structuring lake communities from bacteria to fish. Ecology **87**:

799   2895-2991.

800 Bengtsson, J. 2010. Applied (meta)community ecology: diversity and ecosystem services at

801   the intersection of local and regional processes. In Community Ecology. Processes,

802   Models, and Applications. (eds. Verhoef H.A. and Morin P.J.). Oxford University

803   Press, New York, pp. 115–130.

804 Bhowmik, A. K., and Schäfer, R. B. 2015. Large scale relationship between aquatic insect

805   traits and climate. PLoS ONE **10**: e0130025.

806   Bilton, D.T., Freeland, J.R., and Okamura, B. 2001. Dispersal in freshwater invertebrates.

807   Annual Review of Ecology and Systematics **32**: 159–181.

808   Black, W.R. 2003. Transportation: A geographical analysis. Guilford Press.

809   Blakely, T. J., Harding, J. S., Mcintosh, A. R., and Winterbourn, M. J. 2006. Barriers to the

810   recovery of aquatic insect communities in urban streams. Freshwat. Biol. **51**: 1634-

811   1645.

812   Blanchet, F.G., Legendre, P., and Borcard, D. 2008a. Forward selection of explanatory

813   variables. Ecology **89**: 2623–2632.

814   Blanchet, F. G., Legendre, P., and Borcard, D. 2008b. Modelling directional spatial processes

815   in ecological data. Ecol. Model. **215**: 325-336.

816   Blanchet, F. G., Legendre, P., Maranger, R., Monti, D., and Pepin, P. 2011. Modelling the

817   effect of directional spatial ecological processes at different scales. Oecologia **166:**

818   357-368.

819   Bohmann, K., Evans, A., Gilbert, M. T., Carvalho, G. R., Creer, S., Knapp, M. 2014.

820   Environmental DNA for wildlife biology and biodiversity monitoring. Trends Ecol.

821   Evol. **29:** 358–367.

822   Bohonak, A. J. 1999. Dispersal, gene flow, and population structure. Quart. Rev. Biol. **74**:

823   21-45.

824   Bohonak A. J., and Jenkins D. G. 2003. Ecological and evolutionary significance of dispersal

825   by freshwater invertebrates. Ecol. Lett. **6**: 783-796.

826   Bond, N. R., and Lake, P. S. 2003. Local habitat restoration in streams: Constraints on the

827   effectiveness of restoration for stream biota. Ecol. Manag. Rest. **4**: 193-198.

828   Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of

829   principal coordinates of neighbour matrices. Ecol. Model. **153**: 51–68.

830   Borthagaray, A.I., Berazategui, M., and Arim, M. 2015. Disentangling the effects of local and

831   regional processes on biodiversity patterns through taxon-contingent metacommunity

832   network analysis. Oikos **124:** 1383-1390.

833   Bried, J. T., McIntyre, N. E., Dzialowski, A. R., and Davis, C. A. 2015. Resident-immigrant

834   dichotomy matters for classifying wetland site groups and metacommunities.

835   Freshwat. Biol. **60:** 2248–2260.

836   Brown, B. L., and Swan, C. M. 2010. Dendritic network structure constrains metacommunity

837   properties in riverine ecosystems. J. Anim. Ecol. **79**: 571–580.

838   Brown, B. L., Swan, C. M., Auerbach, D. A., Grant, E. H. C., Hitt, N. P., Maloney, K. O.,

839   and Patrick, C. 2011. Metacommunity theory as a multispecies, multiscale framework

840   for studying the influence of river network structure on riverine communities and

841   ecosystems. J. N. Amer. Benthol. Soc. **30**: 310-327.

842   Calabrese, J. M., and Fagan, W. F. 2004. A comparison-shopper's guide to connectivity

843   metrics. Front. Ecol. Environ. **2**: 529-536.

844   Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever,

845   T. A., and Lytle, D. A. 2015. Dispersal strength determines meta-community structure

846   in a dendritic riverine network. J. Biogeogr. **42**: 778–790.

847   Chu, C., Mandrak, N. E., and Minns, C. K. 2005. Potential impacts of climate change on the

848   distributions of several common and rare freshwater fishes in Canada. Diver. Distr.

849   **11:** 299–310.

850   Clarke R.T., Wright J.F., and Furse M.T. 2003. RIVPACS models for predicting the expected

851   macroinvertebrate fauna and assessing the ecological quality of rivers. Ecol. Model.

852   **160:** 219-233.

853   Cornell H. V., and Harrison S. P. 2014. What are species pools and when are they important?

854   Annu. Rev. Ecol. Evol. Syst. **45**: 45-67.

855   Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community

856   dynamics. Ecol. Lett. **8:** 1175–1182.

857   Cristescu, M. E. 2014. From barcoding single individuals to metabarcoding biological

858   communities. Trends Ecol. Evol. **29:** 566-571.

859   Dale, M. R. T., and Fortin, M.-J. 2010. From graphs to spatial graphs. Annu. Rev. Ecol. Evol.

860   Syst. **41**: 21-38.

861   Datry, T., Bonada, N., and Heino, J. .2016c. Towards understanding the organisation of

862   metacommunities in highly dynamic ecological systems. Oikos **125:** 149-159.

863   Datry, T., Larned, S. T., and Tockner, K. 2014. Intermittent rivers: a challenge for freshwater

864   ecology. BioScience **64**: 229-235.

865   Datry, T., Pella, H., Leigh, C., Bonada, N., and Hugueny, B. 2016a. A landscape approach to

866   advance intermittent river ecology. Freshwat. Biol. **61:** 1200–1213.

867   Datry, T., Melo, A. S., Moya, N., Zubieta, J., De la Barra, E., and Oberdorff, T. 2016b.

868   Metacommunity patterns across three Neotropical catchments with varying

869   environmental harshness. Freshwat. Biol. **61:** 277-292.

870   De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel,

871   H., Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W.,

872   and Declerck, S. A. J. 2012. Body size and dispersal mode as key traits determining

873   metacommunity structure of aquatic organisms. Ecol. Lett. **15**: 740–747.

874 Dijkstra, K. D. B., Monaghan, M. T., and Pauls, S. U. 2014. Freshwater biodiversity and
875   aquatic insect diversification. Annu. Rev. Entomol. **59**: 143-163.

876 Dolédec, S., Philips, N., Scarbrook, M., Riley, R.H., and Townsend C.R. 2006. Comparison
877   of structural and functional approaches to determining land use effects on grassland
878   stream invertebrate communities. J. N. Amer. Benthol. Soc. 25: 44–60.

879 Dray, S., Legendre, P., and Peres-Neto, P. R. 2006. Spatial modelling: a comprehensive
880   framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol.
881   Model. **196**: 483-493.

882 Dray, S., Pélissier, R., Couteron, P., Fortin, M. J., Legendre, P., Peres-Neto, P. R., Bellier, E.,
883   Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A. B., Heegaard, E., Jombart,
884   T., Munoz, F., Oksanen, J., Thiouleuse, J., and Wagner, H. H. 2012. Community
885   ecology in the age of multivariate multiscale spatial analysis. Ecol. Monogr. **82**: 257-
886   275.

887 Duckett, P. E., Wilson, P. D., and Stow, A. J. 2013. Keeping up with the neighbours: using a
888   genetic measurement of dispersal and species distribution modelling to assess the
889   impact of climate change on an Australian arid zone gecko (*Gehyra variegata*).
890   Divers. Distr. **19**: 964-976.

891 Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque,
892   C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., and Sullivan, C.
893   A. (2006) Freshwater biodiversity: importance, threats, status and conservation
894   challenges. Biol. Rev. **81:** 163–182.

895 Erős, T., and Campbell Grant, E. H. 2015. Unifying research on the fragmentation of
896   terrestrial and aquatic habitats: patches, connectivity and the matrix in riverscapes.
897   Freshwat. Biol. **60**: 1487-1501.

898   Erős, T., Olden, J., Schick, S., Schmera, D., and Fortin, M.-J. 2012. Characterising

899   connectivity relationships in freshwaters using patch-based graphs. Lands. Ecol. **27**:

900   303-317.

901   Evans, M. R., Norris, K. J., and Benton, T. G. 2012. Predictive ecology: systems approaches.

902   Phil. Trans. Royal Soc. B **367**: 163-169.

903   Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol.

904   Syst. **34**: 487-515.

905   Fahrig, L., and Merriam, G. 1994. Conservation of fragmented populations. Cons. Biol. **8**:

906   50-59.

907   Farber, S., Neutens, T., Miller, H. J., and Li, X. 2013. The social interaction potential of

908   metropolitan regions: A time-geographic measurement approach using joint

909   accessibility. Ann. Assoc. Amer. Geogr. **103:** 483-504.

910   Fenchel, T., and Finlay B. J. 2004. The ubiquity of small species: Patterns of local and global

911   diversity. Bioscience **54**: 777-784.

912   Filipe, A.F., Markovic, D., Pletterbauer, F., Tisseuil, C., De Wever, A., Schmutz, S., Bonada,

913   N. and Freyhof, J. (2013) Forecasting fish distribution along stream networks: brown

914   trout (*Salmo trutta*) in Europe. Divers. Distr. **19**: 1059-1071.

915   Finn, D. S., Bonada, N., Múrria, C., and Hughes, J. M. 2011. Small but mighty: headwaters

916   are vital to stream network biodiversity at two levels of organization. J. N. Amer.

917   Benthol. Soc. **30**: 963-980.

918   Friberg, N. 2014. Impacts and indicators of change in lotic ecosystems. WIREs Water

919   **1:** 513–531.

920 Friberg, N., Bonada, N., Bradley, D.C., Dunbar, M.J., Edwards, F.K., Grey, J., Hayes, R.B.,

921   Hildrew, A.G., Lamouroux, N., Trimmer, M., and Woodward, G. 2011.

922   Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the

923   ugly. Adv. Ecol. Res. **44:** 1–68.

924 Galpern, P., Manseau, M., and Fall, A. 2011. Patch-based graphs of landscape connectivity: a

925   guide to construction, analysis and application for conservation. Biol. Cons. **144**: 44-

926   55.

927 Garcia-Llorente, M., Martin-Lopez, B., Diaz, S., and Montes, C. 2011. Can ecosystem

928   properties be fully translated into service values? An economic valuation of aquatic

929   plant services. Ecol. Appl. **21:** 3083-3103.

930 Geurs, K. T., and van Wee, B. 2004. Accessibility evaluation of land-use and transport

931   strategies: review and research directions. J. Trans. Geogr. **12**: 127-140.

932 Gilbert, B., and Bennett, J. R. 2010. Partitioning variation in ecological communities: do the

933   numbers add up? J. Appl. Ecol. **47**: 1071–1082.

934 Göthe, E., Angeler, D. G., and Sandin, L. 2013a. Metacommunity structure in a small boreal

935   stream network. J. Anim. Ecol. **82**: 449–458.

936 Göthe, E., Angeler, D. G., Gottschalk, S., Löfgren, S., and Sandin, L. 2013b. The influence of

937   environmental, biotic and spatial factors on diatom metacommunity structure in

938   Swedish Headwater streams. PLoS One **8**: e72237.

939 Grant, E. H. C., Lowe, W. H., and Fagan, W. F. 2007. Living in the branches: population

940   dynamics and ecological processes in dendritic networks. Ecol. Lett. **10**: 165-175.

941 Graves, T., Chandler, R. B., Royle, J. A., Beier, P., and Kendall, K. C. 2014. Estimating

942   landscape resistance to dispersal. Lands. Ecol. **29**: 1201-1211.

943 Gray, D. K., and Arnott, S. E. 2011. Does dispersal limitation impact the recovery of

944   zooplankton communities damaged by a regional stressor? Ecol. Appl. **21**: 1241–

945   1256.

946 Gray, D. K., and Arnott, S. E. 2012. The role of dispersal levels, Allee effects and community

947   resistance as zooplankton communities respond to environmental change. J. Appl.

948   Ecol. **49**: 1216–1224.

949 Griffith, D. A., and Peres-Neto, P. R. 2006. Spatial modeling in ecology: the flexibility of

950   eigenfunction spatial analyses. Ecology **87**: 2603–2613.

951 Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., and Bini, L. M. 2013.

952   Metacommunity structuring in stream networks: roles of dispersal mode, distance

953   type and regional environmental context. Ecol. Evol. **3**: 4473-4487.

954 Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology.

955   Ecol. Model. **135:** 147-186.

956 Havel, J. E., Lee, C. E., and Vander Zanden, J. M. 2005. Do reservoirs facilitate invasions

957   into landscapes? BioScience **55**: 518-525.

958 Harrison, R.G. 1980. Dispersal polymorphism in insects. Annu. Rev. Ecol. Syst. **11:** 95–118.

959 Hawkins, C. P., Norris, R. H., Hogue, J. N., and Feminella, J.W. 2000a.

960   Development and evaluation of predictive

961   models for measuring the biological integrity of streams. Ecological Applications

962   **10**: 1456-1477.

963 Hawkins, C. P., Norris, R. H., Gerritsen, J., Hughes, R. M., Jackson, S. K., Johnson, R. H.,

964   and Stevenson, R. J. 2000b. Evaluation of landscape classifications for biological

965   assessment of freshwater ecosystems: synthesis and recommendations.

966   J. N. Amer. Benthol. Soc. **19**: 541-556.

967 Heffernan, J. B., Soranno, P. A., Angilletta Jr, M.J., Buckley, L. B., Gruner, D. S., Keitt, T.

968   H., Kellner, J. R., Kominoski, J. S., Rocha, A. V., Xiao, J., Harms, T. K., Goring, S.

969   J., Koenig, L. E., McDowell, W. H., Powell, H., Richardson, A. D., Stow, C. A.,

970   Vargas, R., and Weathers, K. C. 2014. Macrosystems ecology: Understanding

971   ecological pattern and process at continental scales. Front. Ecol. Env. **12**: 5-14

972 Heino, J. 2013a. The importance of metacommunity ecology for environmental assessment

973   research in the freshwater realm. Biological Reviews **88**: 166-178.

974 Heino, J. 2013b. Does dispersal ability affect the relative importance of environmental

975   control and spatial structuring of littoral macroinvertebrate communities? Oecologia

976   **171**: 971-980.

977 Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., and Bini, L. M. 2015a.

978   Metacommunity organisation, spatial extent and dispersal in aquatic systems:

979   patterns, processes and prospects. Freshwat. Biol. **60**: 845-869.

980 Heino, J., Melo, A. S., Bini, L. M., Altermatt, F., Al-Shami, S. A, Angeler, D., Bonada, N.,

981   Brand, C., Callisto, M., Cottenie, K., Dangles, O., Dudgeon, D., Encalada, A., Göthe,

982   E., Grönroos, M., Hamada, N., Jacobsen, D., Landeiro, V. L., Ligeiro, R., Martins, R.

983   T., Miserendino, M. L., Md Rawi, C. S. Rodrigues, M., Roque, F. O., Sandin, L.,

984   Schmera, D., Sgarbi, L. F., Simaika, J., Siqueira, T., Thompson, R. M., and

985   Townsend, C. R. 2015b. A comparative analysis reveals weak relationships between

986   ecological factors and beta diversity of stream insect metacommunities at two spatial

987   levels. Ecol. Evol. **5:** 1235-1248.

988   Heino, J., Virkkala, R., and Toivonen, H. (2009) Climate change and freshwater biodiversity:

989   detected patterns, future trends and adaptations in northern regions. Biol. Rev. **84:** 39–

990   54.

991   Hoffsten, P.-O. (2004) Site-occupancy in relation to flight-morphology in caddisflies.

992   Freshwat. Biol. **49:** 810–817.

993   Holland, R. A., Eigenbrod, F., Armsworth, P. R., Anderson, B. J., Thomas, C. D.,

994   Heinemeyer, A., Gillings, S., Roy, D. B., and Gaston, K. J. (2011) Spatial

995   covariation between freshwater and terrestrial ecosystem services. Ecol. Appl. **21:**

996   2034–2048.

997   Holyoak, M., Leibold, M.A., Mouquet, N.M., Holt, R.D., and Hoopes, M.F. 2005.

998   Metacommunities: A framework for large-scale community ecology. In: M. Holyoak,

999   M.A. Leibold, and R. D. Holt (Eds) Metacommunities: Spatial Dynamics and

1000   Ecological Communities. University of Chicago Press, Chicago, pp. 1-31.

1001   Horváth, Z., Vad, C. F., and Ptacnik, R. 2016. Wind dispersal results in a gradient of

1002   dispersal limitation and environmental match among discrete aquatic habitats.

1003   Ecography 39: 726–732.

1004   Hubbell, S.J. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton

1005   University Press, Princeton.

1006   Huff, D. L. 1963. A probabilistic analysis of shopping center trade areas. Land Economics

1007   **39**: 81-90.

1008   Hughes, J. M. 2007. Constraints on recovery: using molecular methods to study connectivity

1009   of aquatic biota in rivers and streams. Freshwat. Biol. **52**: 616-631.

Hughes, J. M., Schmidt, D. J., and Finn, D. S 2009. Genes in streams: Using DNA to understand the movement of freshwater fauna and their riverine habitat. BioScience **59**: 573-583.

Jackson, D. A., Peres-Neto, P. R., and Olden, J. D. 2001. What controls who is where in freshwater fish communities –the roles of biotic, abiotic and spatial factors. Can. J. Fish. Aquat. Sci. **58**: 157-170.

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

Jaeger, K. L., Olden, J. D., and Pelland, N. A. (2014) Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proc. Nat. Acad. Sci. **111**: 13894-13899.

Jenkins, D.G., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R. 2007. Does size matter for dispersal distance? Glob. Ecol. Biogeogr. **16:** 415–425.

Joly, P., Miaud, C., Lehmann, A., and Grolet, O. 2001. Habitat matrix effects on pond occupancy in newts. Conserv. Biol. **15**: 239-248.

Jones, N. T., Germain, R. M., Grainger, T. N., Hall, A. M., Baldwin, L., and Gilbert, B. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. J. Ecol. **103:** 935–944.

Kärnä, O.-M. 2014. Effects of spatial location, environmental factors and species dispersal ability on invertebrate community structure in subarctic streams. MSc thesis, Department of Geography, University of Oulu. [In Finnish]

1032 Kärnä, O.-M., Grönroos, M., Antikainen, H., Hjort, J., Ilmonen, J., Paasivirta, L., and Heino,

1033   J. 2015. Inferring the effects of potential dispersal routes on the metacommunity

1034   structure of stream insects: as the crow flies, as the fish swims or as the fox runs? J.

1035   Anim. Ecol. **84**: 1342-1353.

1036 Kristiansen, J. 1996. Dispersal by freshwater algae – a review. Hydrobiologia **336**: 151–157.

1037 Kwan, M. P. 1998. Space-time and integral measures of individual accessibility: a

1038   comparative analysis using a point-based framework. Geogr. Anal. **30**: 191-216.

1039 Landeiro, V. L., Magnusson, W. E., Melo, A. S., Espirito-Santo, H. M. V., and Bini L. M.

1040   2011. Spatial eigenfunction analyses in stream networks: do watercourse and overland

1041   distances produce different results? Freshwat. Biol. **56**: 1184-1192.

1042 Landeiro, V.L., Bini, L.M., Melo, A.S., Pes, A.M.O., and Magnusson, W.E. 2012. The roles

1043   of dispersal limitation and environmental conditions in controlling caddisfly

1044   (Trichoptera) assemblages. Freshwat. Biol. **57:** 1554-1564.

1045 Larkin, J. L., Maehr, D. S., Hoctor, T. S., Orlando, M. A., and Whitney, K. 2004. Landscape

1046   linkages and conservation planning for the black bear in west-central Florida. Anim.

1047   Conserv. **7**: 23-34.

1048 LaRue, M.A., and Nielsen, C.K. 2008. Modelling potential dispersal corridors for cougars in

1049   midwestern North America using least-cost path methods. Ecol. Model. **212**: 371–

1050   381.

1051 Layeghifard, M., Makarenkov, V., and Peres-Neto, P. R. 2015. Spatial and species

1052   compositional networks for inferring connectivity patterns in ecological communities.

1053   Glob. Ecol. Biogeogr. **24**: 718-727.

1054 Lechner, A. M., Doerr, V., Harris, R. M., Doerr, E., and Lefroy, E. C. 2015. A framework for

1055   incorporating fine-scale dispersal behaviour into biodiversity conservation planning.

1056   Lands. Urb. Plan. **141**: 11-23.

1057 Legendre, P. 2014. Interpreting the replacement and richness difference components of beta

1058   diversity. Glob. Ecol. Biogeogr. **23**: 1324-1334.

1059 Legendre, P., and Legendre, L. 2012. Numerical Ecology. Third Edition. Elsevier,

1060   Amsterdam.

1061 Leibold, M.A. Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M. F.,

1062   Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004.

1063   The metacommunity concept: a framework for multi-scale community ecology.

1064   Ecol. Lett. **7:** 601-613.

1065 Leibold, M. A., and Loeuille, N. 2015. Species sorting and patch dynamics in harlequin

1066   metacommunities affect the relative importance of environment and space. Ecology

1067   **96:** 3227-3233.

1068 Lennon, J. J., Koleff, P., Greenwood, J. J. D., and Gaston, K. J. 2001. The geographical
1069   structure of British bird distributions: diversity, spatial turnover and scale. J. Anim.
1070   Ecol. **70**: 966-979.

1071 Liu, J., Soininen, J., Han, B-P., and Declerck, S. A. J. 2013. Effects of connectivity, dispersal

1072   directionality and functional traits on the metacommunity structure of river benthic

1073   diatoms. J. Biogeogr. **40**: 2238–2248.

1074 Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H. and The Metacommunity Working

1075   Group. 2011. Empirical approaches to metacommunities: a review and comparison

1076   with theory. Trends Ecol. Evol. **26**: 482-91.

1077 Lowe, W. H., and McPeek, M. A. 2014. Is dispersal neutral? Trends Ecol. Evol. **29**: 444-450.

1078 Macneale, K.H.; Peckarsky, B.L, and Likens, G.E. 2005. Stable isotopes identify dispersal

1079   patterns of stonefly populations living along stream corridors. Freshwat. Biol. **50:**

1080   1117-1130.

1081 Magnuson, J. J., Tonn, W. M., Banerjee, A., Toivonen, J., Sanchez, O., and Rask, M. 1998.

1082   Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology **79**:

1083   2941–2956.

1084 Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies

1085   (Plecoptera) and mayflies (Ephemeroptera)? Biol. Cons. 93: 271–276.

1086 Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. Freshwat. Biol. **47:** 679–

1087   694.

1088 Maloney, K. O., and Munguia, P. 2011. Distance decay of similarity in temperate aquatic

1089   communities: effects of environmental transition zones, distance measure, and life

1090   histories. Ecography **34**: 287–295.

1091 Manel, S., and Holderegger, R. 2013. Ten years of landscape genetics. Trends Ecol. Evol. **28:**

1092   614-621.

1093 Manel, S., Schwartz, M., Luikart, G., and Taberlet, P. 2003. Landscape genetics: combining

1094   landscape ecology and population genetics. Trends Ecol. Evol. **20:** 136-142.

1095 Mantel, N. 1967. The detection of disease clustering and a generalized regression approach.

1096   Canc. Res. **27**: 209–220.

1097 Margules, C. R., and Pressey, R. L. 2000. Systematic conservation planning. Nature **405**:

1098   243-253.

1099 Matthews, J. W. 1998. Patterns in Freshwater Fish Ecology. Chapman and Hall, New York.

1100   McRae, B. H. 2006. Isolation by landscape resistance. Evolution **60:** 1551-1561.

1101   McRae, B. H., Hall, S. A., Beier, P., and Theobald, D. M. 2012. Where to restore ecological

1102   connectivity? Detecting barriers and quantifying restoration benefits. PLoS ONE **7:**

1103   e52604.

1104   Merritt, R. W., Cummins, K. W., and Berg, M. B. 2008. An Introduction to the Aquatic

1105   Insects of North America. Fourth Edition. Kendall/Hunt Publishing Company,

1106   Dubuque.

1107   Monteiro, V. F., Paiva, P. C., and Peres-Neto, P. R. 2017. A quantitative framework to

1108   estimate the relative importance of environment, spatial variation and patch

1109   connectivity in driving community composition. J. Anim. Ecol. **86:** 316–326.

1110   Mouquet, N., and Loreau, M. 2003. Community patterns in source-sink metacommunities.

1111   Am. Nat. **162**: 544-557.

1112   Nabout, J.C., Siqueira,T., Bini, L.M., and Nogueira, I.S. (2009) No evidence for

1113   environmental and spatial processes in structuring phytoplankton communities. Acta

1114   Oecol. **35:** 720-726.

1115   Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P. E.

1116   2008. A movement ecology paradigm for unifying organismal movement research.

1117   Proc. Nat. Acad. Sci. **105**: 19052-19059.

1118   Nekola, J. C., and White, P. S. 1999. The distance decay of similarity in biogeography and

1119   ecology. J. Biogeogr. **26**: 867-878.

1120   Ng, I. S. Y., Carr, C., and Cottenie, K. (2009) Hierarchical zooplankton metacommunities:

1121   distinguishing between high and limiting dispersal mechanisms. Hydrobiologia **619**:

1122   133-143.

1123 Olden, J., Jackson, D. A., and Peres-Neto, P. R. 2001. Spatial isolation and fish communities

1124   in drainage lakes. Oecologia **127**: 572-585.

1125 Orsini, L., Vanoverbeke, J., Swillen, I., Mergeay, J., and De Meester, L. (2013) Drivers of

1126   population genetic differentiation in the wild: isolation by dispersal limitation,

1127   isolation by adaptation and isolation by colonization. Mol. Ecol. **22**: 5983-5999.

1128 Padial, A.A., Ceschin, F., Declerck, S.A.J., De Meester, L., Bonecker, C.C. 2014. Dispersal

1129   ability determines the role of environmental, spatial and temporal drivers of

1130   metacommunity structure. PLoS ONE **9:** e111227.

1131 Páez, A., Scott, D. M., and Morency, C. 2012. Measuring accessibility: positive and

1132   normative implementations of various accessibility indicators. J. Trans. Geogr. **25**:

1133   141-153.

1134 Palmer, M. A., Allan, J. D., and Butman, C. A. 1996. Dispersal as a regional process

1135   affecting the local dynamics of marine and stream benthic invertebrates. Trends Ecol.

1136   Evol. **11**: 322–326.

1137 Pärtel, M., Szava-Kovats, R., and Zobel, M. 2011. Dark diversity: shedding light on absent

1138   species. Trends Ecol. Evol. **26**: 124–128.

1139 Pelicice, F. M., and Agostinho, A. A. 2008. Fish-passage facilities as ecological traps in large

1140   Neotropical rivers. Cons. Biol. **22**: 180-188.

1141 Pereira, M., Segurado, P., and Neves, N. 2011. Using spatial network structure in landscape

1142   management and planning: A case study with pond turtles. Lands. and Urb. Plan. **100**:

1143   67-76.

1144 Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. 2006. Variation partitioning of
1145   species data matrices: estimation and comparison of fractions. Ecology **87:** 2614-
1146   2625.

1147 Peres-Neto, P. R., and Legendre, P. 2010. Estimating and controlling for spatial structure in
1148   the study of ecological communities. Glob. Ecol. Biogeogr. **19:** 174-184.

1149 Petchey, O. L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara,
1150   G. M., Altermatt, F., Matthews, B., Levine, J. M., Childs, D. Z., McGill, B. J.,
1151   Schaepman, M. E., Schmid, B., Spaak, P., Beckerman, A. P., Pennekamp, F., and
1152   Pearse, I. S. 2015. The ecological forecast horizon, and examples of its uses and
1153   determinants. Ecol. Lett. **18**: 597-611.

1154 Peterson, E. E., Theobald, D. M., and Ver Hoef, J. M. 2007. Geostatistical modelling on
1155   stream networks: developing valid covariance matrices based on hydrological
1156   distance and stream flow. Freshwat. Biol. **52**: 267-279.

1157 Pinto, N., and Keitt, T. H. 2009. Beyond the least-cost path: evaluating corridor redundancy
1158   using a graph theoretic approach. Lands. Ecol. **24:** 253-266.

1159 Poff, N. L., Olden, J. D., and Strayer, D. L. 2012. Climate change and freshwater fauna
1160   extinction risk. In Saving A Million Species. Extinction Risk From Climate Change.
1161   Washington, DC, Island Press, pp. 309-336.

1162 Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P., and Kondratieff, B.C.
1163   2006. Functional trait niches of North American lotic insects: trait-based ecological
1164   applications in light of phylogenetic relationships. J. N. Amer. Benthol. Soc. **25:** 730-
1165   755.

1166 Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. **132:** 652-661.

1167 Rayfield, B., Fortin, M.-J., and Fall, A. 2011. Connectivity for conservation. A framework to
1168   classify network measures. Ecology **92**: 847-858.

1169 Relethford, J. H. 2004. Boas and beyond: Migration and craniometric variation. American J.
1170   Hum. Biol. **16:** 379–386.

1171 Ridley, M. 2004. Crick and Darwin's shared publication in Nature. Nature **431**: 244-244.

1172 Rietveld, P., and Bruinsma, F. R. 1998. Is Transport Infrastructure Effective? Transport
1173   Infrastructure and Accessibility: Impacts on the Space Economy. Springer.

1174 Riis, T., and Sand-Jensen, K. 2006. Dispersal of plant fragments in small streams. Freshwat.
1175   Biol. **51**: 274-286.

1176 Rouquette, J. R., Dallimer, M., Armsworth, P. R., Gaston, K. J., Maltby, L., and Warren, P.
1177   H. 2013. Species turnover and geographic distance in an urban river network. Divers.
1178   Distr. **19**: 1429-1439.

1179 Rundle, S. D., Bilton, D. T., and Foggo, A. 2007. By wind, wings or water: body size,
1180   dispersal and range size in aquatic invertebrates. Body size: The Structure and
1181   Function of Aquatic Ecosystems (ed. by A. G. Hildrew, D. G. Raffaelli and R.
1182   Edmonds-Brown), pp. 186-209. Cambridge University Press, Cambridge.

1183 Sarremejane, R., Mykrä, H., Bonada, N., Aroviita J., and Muotka, T. (2017) Habitat connectivity and
1184   dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river
1185   networks. Freshwat. Biol. https://doi.org/10.1111/fwb.12926.

1186 Saura, S., Bodin, Ö., and Fortin, M.-J. 2014. Stepping stones are crucial for species' long-
1187   distance dispersal and range expansion through habitat networks. J. Appl. Ecol. **51:**
1188   171–182.

1189 Saura, S., and Rubio, L. 2010. A common currency for the different ways in which patches
1190   and links can contribute to habitat availability and connectivity in the landscape.
1191   Ecography **33:** 523-537.

1192 Sawyer, S. C., Epps, C. W., and Brashares, J. S. 2011. Placing linkages among fragmented
1193   habitats: do least-cost models reflect how animals use landscapes? J. Appl. Ecol.
1194   **48:** 668–678.

1195 Sekar, S. 2012. A meta–analysis of the traits affecting dispersal ability in butterflies: can
1196   wingspan be used as a proxy? J. Anim. Ecol. **81**: 174-184.

1197 Shurin, J. B., Cottenie, K., and Hillebrand, H. 2009. Spatial autocorrelation and dispersal
1198   limitation in freshwater organisms. Oecologia **159**: 151-159.

1199 Silva, P. G. da, and Hernández, M. I. M. 2014. Local and regional effects on community
1200   structure of dung beetles in a mainland-island scenario. PLoS ONE **9:** e111883.

1201 Siqueira, T., Durães, L. D., and Roque, F. O. 2014. Predictive modelling of insect
1202   metacommunities in biomonitoring of aquatic networks. In C. P. Ferreira and W. A.
1203   C. Godoy (Eds). Ecological modelling applied to entomology. Springer.

1204 Smith, R. F., Alexander, L. C., and Lamp, W. O. 2009. Dispersal by terrestrial stages of
1205   stream insects in urban watersheds: a synthesis of current knowledge. J. N. Amer.
1206   Benthol. Soc. **28**: 1022-1037.

1207 Smith, T. W., and Lundholm, J. T. 2010. Variation partitioning as a tool to distinguish
1208   between niche and neutral processes. Ecography **33:** 648–655.

1209 Smoyer-Tomic, K. E., Spence, J. C., and Amrhein, C. 2006. Food deserts in the prairies?
1210   Supermarket accessibility and neighborhood need in Edmonton, Canada. Prof. Geogr.
1211   **58:** 307-326.

1212 Soininen, J. 2014. A quantitative analysis of species sorting across organisms and

1213   ecosystems. Ecology **95**: 3284-3292.

1214 Soininen, J. 2016. Spatial structure in ecological communities–a quantitative analysis. Oikos

1215   **125:** 160-166.

1216 Soininen, J., McDonald, R., and Hillebrand, H. (2007) The distance decay of similarity in

1217   ecological communities. Ecography **30**: 3-12.

1218 Soulé, M. E. 1985. What is conservation biology? BioScience **35**: 727–734.

1219 Sutherland, C., Fuller, A. K., and Royle, J. A. 2015. Modelling non-Euclidean movement and

1220   landscape connectivity in highly structured ecological networks. Methods Ecol. Evol.

1221   **6**, 169–177.

1222 Tachet, H., Richoux, P., Bournaud, M., and Usseglio-Polatera, P., 2010. Invertébrés d'eau

1223   douce: Systématique, biologie, écologie, 3rd ed. CNRS éditions, Paris.

1224 Tesson, S.V.M., and Edelaar, P. 2013. Dispersal in a changing world: opportunities, insights

1225   and challenges. Mov. Ecol. 1**:** 10.

1226 Thompson, R.M., and Townsend, C.R. 2006. A truce with neutral theory: local deterministic

1227   factors, species traits and dispersal limitation together determine patterns of diversity

1228   in stream invertebrates. J. Anim. Ecol. **75:** 476-484.

1229 Thuiller, W., Münkemüller, T, Lavergne, S., Mouillot, D., Mouquet, N., Schiffers, K., and

1230   Gravel, D. 2013. A road map for integrating eco-evolutionary processes into

1231   biodiversity models. Ecol. Lett. **16**: 94-105.

1232 Tobler, W. 1970. A computer movie simulating urban growth in the Detroit region. Econ.

1233   Geogr. **46**: 234-240.

1234 Tolonen, K.T., Hämäläinen, H., Holopainen, I.J., Mikkonen, K., and Karjalainen, J. 2003.

1235   Body size and substrate association of littoral insects in relation to vegetation

1236   structure. Hydrobiologia **499:** 179-190.

1237 Tomanova, S., and Usseglio-Polatera, P. 2007. Patterns of benthic community traits in

1238   neotropical streams: relationship to mesoscale spatial variability. Fund. Appl. Limnol.

1239   170: 243–255.

1240 Tonkin, J. D., Stoll, S., Sundermann, A., and Haase, P. 2014. Dispersal distance and the pool

1241   of taxa, but not barriers, determine the colonisation of restored river reaches by

1242   benthic invertebrates. Freshwat. Biol. **59**: 1843–1855.

1243 Tonn, W. M., and Magnuson, J. J. 1982. Patterns in the species composition and richness of

1244   fish assemblages in Northern Wisconsin lakes. Ecology **63**: 1149–1166.

1245 Urban, D., and Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective.
1246   Ecology **82**: 1205-1218.

1247 Urban, D. L., Minor, E. S., Treml, E. A., and Schick, R. S. 2009. Graph models of habitat
1248   mosaics. Ecol. Lett. **12**: 260-273.

1249 Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans,
1250   E. J. 2014. Assessing the relative importance of neutral stochasticity in ecological
1251   communities. Oikos **123**: 1420-1430.

1252 Vasas, V., Magura, T., Jordan, F., and Tothmérész, B. 2009. Graph theory in action:
1253   evaluating planned highway tracks based on connectivity measures. Lands. Ecol. **24:**
1254   581-586.

1255 Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P.,
1256   Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., and Davies, P. M. 2010.
1257   Global threats to human water security and river biodiversity. Nature **467**: 555–561.

1258 Wang I. J., Savage W. K., and Shaffer H. B. 2009. Landscape genetics and GIS least cost

1259   path analysis reveal unexpected dispersal routes in the California tiger salamander,

1260   *Ambystoma californiense*. Mol. Ecol. **18:** 1365-1374.

1261 Weinstein, B. G., Tinoco, B., Parra, J. L., Brown, L. M., McGuire, J. A., Stiles, F. G., and

1262   Graham, C. H. (2014) Taxonomic, phylogenetic, and trait beta diversity in South

1263   American hummingbirds. Am. Nat **184**: 211-224.

1264 Wiens, J. J. 2015. Faster diversification on land than sea helps explain global biodiversity

1265   patterns among habitats and animal phyla. Ecol. Lett. **18**: 1234-1241.

1266 Wilcock, H. R., Hildrew, A. G., and Nichols, R. A. 2001. Genetic differentiation of a

1267   European caddisfly: Past and present gene flow among fragmented larval habitats.

1268   Mol. Ecol. **10**: 1821–1834.

1269 Winegardner, A. K., Jones, B. K., Ng, I. S. Y., Siqueira, T., and Cottenie, K. 2012. The

1270   terminology of metacommunity ecology. Trends Ecol. Evol. **27**: 253-254.

1271 Winemiller, K.O., McIntyre , P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S.,

1272   Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., Stiassny, M.L.J., Silvano, R.A.M.,

1273   Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Petrere

1274   Jr., M., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C., Sousa, L.M., Koning,

1275   A.A., Hoeinghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Petry, P., Zuanon,

1276   J., Torrente Vilara, G., Snoeks, J., Ou, C., Pavanelli, C.S., Akama, A., van

1277   Soesbergen, A. and Sáenz, L. 2016. Balancing hydropower and biodiversity in the

1278   Amazon, Congo, and Mekong. Science **351**: 128-129.

1279 Wisz, M. S., Pottier, J., Kissling, W. D., Pellissier, L., Lenoir, J., Damgaard, C. F., Dormann,

1280   C. F., Forchhammer, M. C., Grytnes, J.-A., Guisan, A., Heikkinen, R. K., Høye, T. T.,

1281   Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E.,

1282   Schmidt, N. M., Termansen, M., Timmermann, A., Wardle, D. A., Aastrup, P., and

1283   Svenning, J.-C. 2013. The role of biotic interactions in shaping distributions and

1284   realised assemblages of species: implications for species distribution modelling. Biol.

1285   Rev. **88**: 15–30.

1286   Wright, J. F., Sutcliffe, D. W., and Furse, M. T. (Eds) 2000. Assessing the biological quality

1287   of fresh waters: RIVPACS and other techniques. Freshwater Biological Association,

1288   Ambleside, UK.

1289   Xie, F., and Levinson, D. 2007. Measuring the structure of road networks. Geogr. Anal. **39,**

1290   336-356.

1291   Zeller, K.A., McGarical, K., and Whiteley, A. R. 2012. Estimating landscape resistance to

1292   movement: a review. Lands. Ecol. **27**: 777-797.

1293   Zeuss, D., Brunzel, S., and Brandl, R. 2017. Environmental drivers of voltinism and body

1294   size in insect assemblages across Europe. Global Ecol. Biogeogr. 26: 154-165.

Table 1. Comparisons of the pros and cons of different dispersal proxies available to study metacommunities.

Dispersal proxy	Pros	Cons
Organismal-based proxies	More closely related to organisms' traits and thus dispersal per se than physical distances between sites.	Often very coarse measures, as sufficient autecological information is available only for a few species or a few organismal groups.
1. Body size	Very easily obtainable for most organismal groups.	Although body size may be related to dispersal mode and capacity, it is also related to many, if not most, other organismal characteristics and functions.
2. Dispersal mode	Rather easily available information for comparisons of broad organismal groups.	Dispersal mode may not effectively relate to actual dispersal distances or dispersal rates between sites.
3. Dispersal ability	Has a strong link to dispersal distances of organisms among sites.	Difficult to obtain information for most organismal groups that cannot be easily tracked.
4. Population genetic structure	Are more direct measures than other organismal-based proxies, and may reveal complex dispersal routes between sites.	Genetic structure can be a biased proxy of dispersal because it not only informs about gene flow among populations, but also about mutation, genetic drift, adaptation by natural selection along environmental gradients and colonization history (i.e. founder effects). Hardly

feasible for a high number of species at the same time.

Graph-based proxies

A. Physical distance-based proxies	Easily measurable from maps when available.	Are coarse proxies that may not always portray true dispersal routes for many species.
1. Euclidean distance	Very easily measurable as shortest linear distance between sites.	Not applicable for organisms, such as fish, relying exclusively on riverine corridors for dispersal.
2. Network distance	Distance between sites in a network may be useful if dispersal is restricted to such networks (e.g. riverine networks for obligatory aquatic organisms).	Some species may show more or less unexpected 'out-of-network' dispersal, which cannot be portrayed by network distances between sites.
3. Flow distance	May well model a) upstream vs downstream dispersal in riverine systems or b) headwind vs. tailwind dispersal in terrestrial systems.	It is not always known for how large a portion of species upstream/headwind dispersal is more costly than downstream/tailwind dispersal.
4. Topographical distance	May sometimes model well altitudinal features that may either prevent or facilitate dispersal. Rather easy to obtain from maps using geographic information systems (GIS).	Topographic features in a landscape may be important for terrestrial animals, but may be less important for those able to fly and cross higher landscape features.
5. Cost distances	May be used to model more complex landscape features	Sometimes lack of suitable maps may prevent

	than just topographic characteristics in a landscape. Potentially may be well used to model dispersal routes in heterogeneous landscapes.	calculating more complex cost distances between sites. Also, what, how and when to consider a landscape feature suitable or not suitable for dispersal may be difficult.
B. Transport geography proxies	Network-specific proxies which can be enhanced by route geometry, travel cost attributes, and pulling and pushing factors, when suitable data are available	Needs topologically correct data and careful calibration of routing data or algorithm, when environment or population specific attributes are applied.
1. Access to network	A simple, binary indicator.	A highly coarse indicator, dependent on how network geometry and connectivity are defined and specified in the first place.
2. Direct network connections or links	A comprehensible indicator expressing the presence of neighbouring localities which can be accessed without passing through other location.	A coarse indicator which does not indicate the distances that need to be travelled.
3. Travel cost to (nearest) destination	A comprehensible indicator expressing the proximity to other locations.	Cannot consider the quality and quantity of accessed locations.
4. Cumulated opportunities	Represents the quantity of accessible locations within a predefined network distance.	The indicator is strongly dependent on the threshold value, and does not take gradual distance decay into account.
5. Potential accessibility, gravity-based	Represents the quantity of accessible locations while taking	The definition of the distance decay function and

measures	into account the distance decay associated with travelling in the network, and the attraction of the location.	the attraction values may be difficult.
6. Population attraction and competition between destinations	Allows the determination of the probability for selecting a given destination while taking the distance decay associated with traversal in the network into account.	The definition of the distance decay function and the attraction values may be difficult.

Table 2. Characteristics of transport geographic accessibility measures (for additional information, see Huff 1963; Kwan 1998; Rietveld and Bruinsma 1998; Páez et al. 2012) and their potential applicability as dispersal proxies in metacommunity ecology.

Accessibility measure/index (Reference in figure 2)	Description	Formulae* for accessibility	Example case in transport geographic context	Examples of potential applications in metacommunity ecology
Access to network (A)	Access or connectivity exists or not	$c = \begin{cases} 0 \ if \ not \ connected \\ 1 \ if \ connected \end{cases}$	To get value 1, city has to be connected to railway network.	Value 1 indicates that the ecological entity** of a locality is connected to the network.
Direct network connections or links (B)	Number of direct connections or links to other nodes in the network	$a = \sum_{j=1}^{n} c_{ij}\,,$ $c = \begin{cases} 0 \ if \ c \ is \ indirect \\ 1 \ if \ c \ is \ direct \end{cases}$	Amount of direct railway links that connect city to other cities.	Number of direct links connecting particular ecological entity** to other communities. E.g. number of species' direct connections to other populations in the dispersal network, which can, for example, consist of streams or terrestrial paths. Value 0 indicates isolated populations, having no direct connections. E.g. headwater streams are linked simply to the downstream reach, whereas confluences are linked to three stream reaches (two upstream and one downstream reaches).

Travel cost to (nearest) destination (C)	Least cost path to (most accessible) object	$a = 1/d$	Travel cost (e.g. time or distance) from the city to the nearest other city.	Travel cost (e.g. time or distance) for fish through riverine corridors from a lake to the nearest other lake. Travel cost (e.g. time or distance) for a vertebrate through ecological corridors from one protected area to another.
Cumulated opportunities (D)	Number of objects within defined travel cost threshold	$a = \sum_{j=1}^{n} A_j \times d_{ij},$ $d = \begin{cases} 0 \ if \ d \geq cost \ threshold \\ 1 \ if \ d < cost \ threshold \end{cases}$	Number of other cities within certain travel cost.	Number of localities within certain travel cost for actively or passively dispersing aquatic, semi-aquatic or terrestrial organisms. Species opportunities to reach other populations (or communities or metacommunities) through dispersal network depending on species dispersal abilities. Cost-distance attributes and thresholds may be specified in relation to the characteristics of the ecological entity**
Potential accessibility, gravity based	High and/or close opportunities	$a = \sum_{j=1}^{n} A_j \times e^{-\beta d_{ij}}$	Potential for interaction with other cities in relation to distance, attraction attributes	An insect female's potential to reach suitable habitats in relation to travel cost to other populations within its lifespan. Here, lifespan

| measures (E) | provide better potential for interaction in comparison to low and/or distant opportunities | | and interests to move. | can be understood as a species' ability or interest to move in relation to travel cost that can vary during a season (term β in formula). |
| Population attraction and competition between destinations (F) | Probability for selecting an attraction amongst all attractions in the space in competitive situation | $P_{ij} = \dfrac{A_j^\alpha d_{ij}^{-\beta}}{\sum_{j=1}^{n} A_j^\alpha d_{ij}^{-\beta}}$ | Amount of interaction with a specific city in relation to other cities, by taking distance, attraction attribute and interests to move into account. | Amount of interaction among habitats with variable environmental quality for female insect or migratory bird individuals from a certain population in relation to travel cost within its lifespan. Here, lifespan can be understood as a species' ability or interest to move in relation to travel cost that can vary during a season (term β in formula). |

* Explanation of terms used in formulations: **a** is accessibility related for each origin, c is connecting link between origin and destination nodes, *d* is travel cost (e.g. distance, time or other measurable friction) between origin and destination nodes, *n* is number of destination nodes, *A_j* is attribute wanted to be accessed in destination(s) (e.g. quantified habitat attraction), *i* refers to (number of) origin and *j* to destination and *β* is parameter for interest to move in relation to travel cost.

** May be an organism, a species, a group of species (i.e. a community), a specific habitat or a biome.

Table 3. Number of articles (*n*) retrieved according to the Web of Science database (from 01/01/2004 to 26/08/2016) using different combinations of keywords related to the use of dispersal proxies in metacommunity studies.

Proxies	keywords	*n*
Organismal-based proxies	"Body size*" AND Dispers* AND metacommunit*	41
	"Dispersal mode*" AND Dispers* AND metacommunit*	43
	"Dispersal capacit*" OR "Dispersal abilit*" AND Dispers* AND metacommunit*	94
	genetic* AND Dispers* AND metacommunit*	45
Physical distance-based proxies	"euclid* distance*" AND Dispers* AND metacommunit*	6
	"network* distance*" AND Dispers* AND metacommunit*	0
	"watercourse distance*" AND Dispers* AND metacommunit*	9
	"flow distance*" AND Dispers* AND metacommunit*	0
	"Topographic* distance*" AND Dispers* AND metacommunit*	0
	"cost distance*" AND Dispers* AND metacommunit*	2
	Mantel AND Dispers* AND metacommunit*	22
	"Spatial eigenfunction*" AND Dispers* AND metacommunit*	5
	"Moran* Eigenvector*" AND Dispers* AND metacommunit*	3
	"principal coordinates of neighbor matrices" AND Dispers* AND metacommunit*	1
Transport geography proxies	"Access to network*" AND Dispers* AND metacommunit*	0
	"Direct network* connection*" AND Dispers* AND metacommunit*	0
	"Travel* cost*" AND Dispers* AND metacommunit*	0
	"Cumulat* opportunit*" AND Dispers* AND metacommunit*	0
	"Potential accessibility" AND Dispers* AND metacommunit*	0

Figure captions

Fig. 1. A schematic figure of potential dispersal routes for species in dendritic systems (light blue colour) among three sites (red dots). **A** describes Euclidean (orange), overland (green) and watercourse (blue) distances; **B** describes cost distance as related to topography (brown) and stream flow resistance (blue); **C** describes two species (light green vs dark green) which have different optimal dispersal routes between sites in relation to the cost imposed by land cover or land use; and **D** describes two optimal dispersal routes for a species in response to the dominant wind direction.

Fig. 2. A schematic figure of transport geographic accessibility measures (Huff 1963; Kwan 1998; Rietveld and Bruinsma 1998; Páez et al. 2012) and their potential applicability as ecological dispersal proxies. The letters (A-F) correspond to the description of the measures of accessibility in Table 2.

Fig. 3. An example of different physical and organismal dispersal proxies in stream insect research (figures redrawn based on results in Kärnä, 2014 and Kärnä et al. 2015). Mantel correlations between Bray-Curtis biological community dissimilarities and environmental distances (based on various local environmental variables) or each of the four types of physical distances are shown. Separate analyses were run for all species, different body size classes and dispersal modes (active or passive). Asterisk indicates a significant correlation. In these data, environmental and physical distances were not strongly correlated, and partial Mantel test were hence very similar to these Mantel tests shown here. See text for further information.
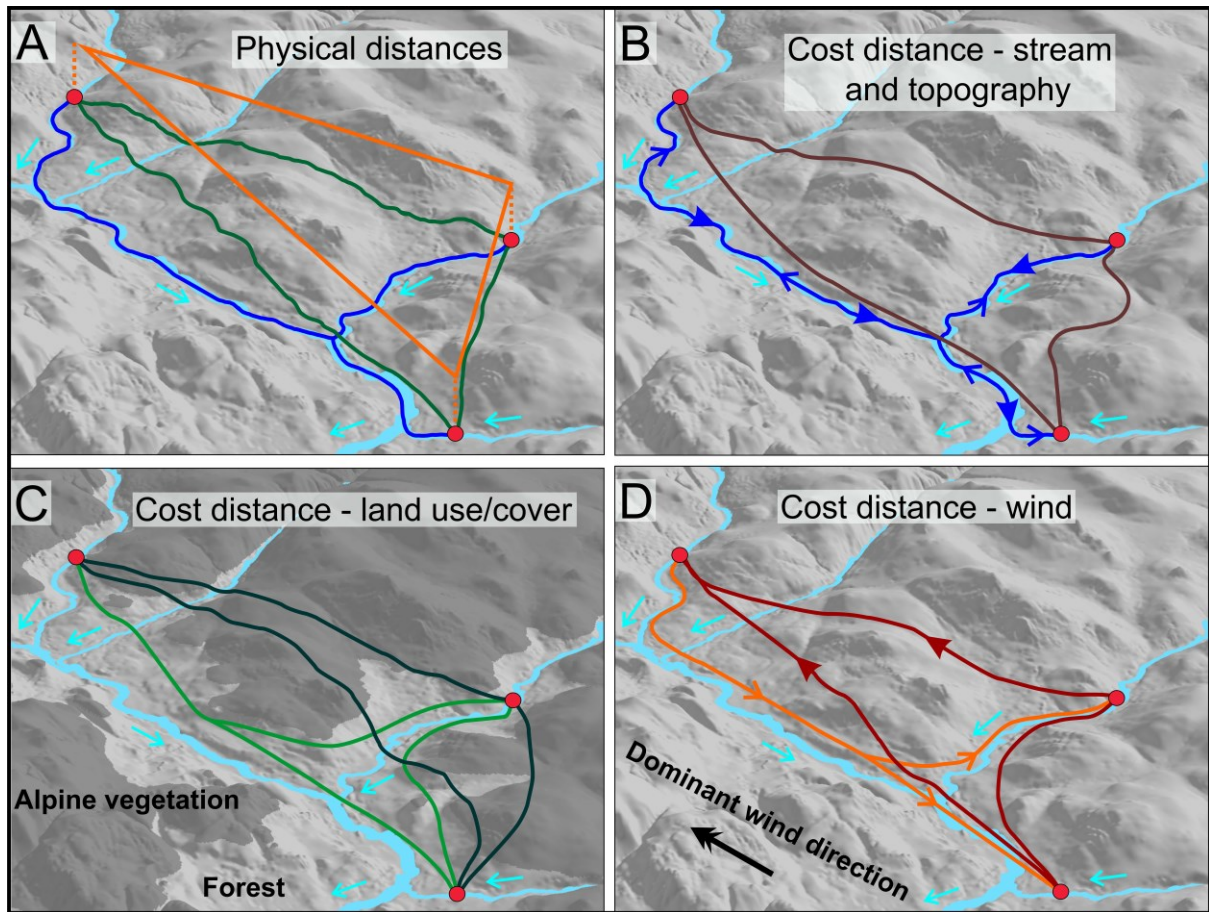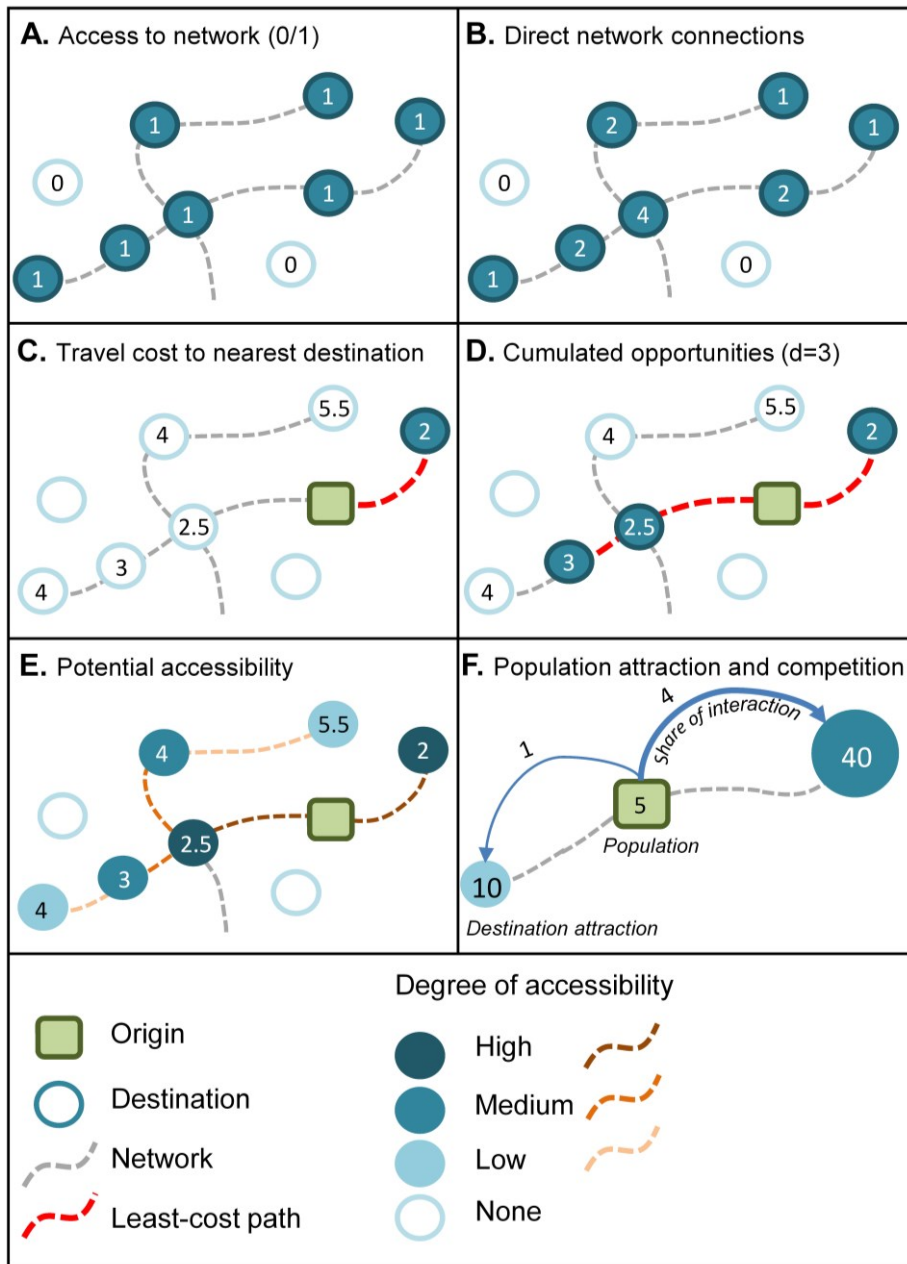
Fig. 1.

A   Physical distances

B   Cost distance - stream and topography

C   Cost distance - land use/cover

Alpine vegetation

Forest

D   Cost distance - wind

Dominant wind direction

Fig. 2.

Fig. 3.