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

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1 **Integrating dispersal proxies in ecological and environmental research in**

2 **the freshwater realm**

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4 Jani Heino[1], Janne Alahuhta[2], Terhi Ala-Hulkko[2], Harri Antikainen[2], Luis Mauricio Bini[3],

5 Núria Bonada[4], Thibault Datry[5], Tibor Erős[6], Jan Hjort[2], Ossi Kotavaara[2], Adriano S. Melo[3]

6 and Janne Soininen[7]

7

8 [1]Finnish Environment Institute, Natural Environment Centre, Biodiversity, Paavo Havaksen

9 Tie 3, FI-90570 Oulu, Finland.

10 [2]University of Oulu, Geography Research Unit, P.O. Box 3000, FI-90014 Oulu, Finland.

11 [3]Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, 74001-970, GO, Brazil.

12 [4]Grup de Recerca Freshwater Ecology and Management (FEM), Departament d'Ecologia,

13 Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona

14 (UB), Diagonal 643, 08028-Barcelona, Catalonia, Spain.

15 [5]IRSTEA, UR-MALY, 5 rue de la Doua, BP 32108, 69616 VILLEURBANNE Cedex,
16 France.

17 [6]Balaton Limnological Institute, MTA Centre for Ecological Research, Klebelsberg K. u. 3.,

18 H-8237 Tihany, Hungary.

19 [7]University of Helsinki, Department of Geosciences and Geography, P.O. Box 64, FI-00014

20 Helsinki, Finland.

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22   Email: jani.heino@environment.fi

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24   ABSTRACT

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

40   taken into account.

41

42   *Key words*: accessibility, bioassessment, connectivity, conservation, dispersal, freshwater,

43   links, metacommunity, nodes, transport geography.

44

45

Introduction

47

48 Ever since Charles Darwin, ecologists have been interested in dispersal (Ridley 2004), i.e.,

49 the movement of an organism from one location to another. Dispersal is one of the most

50 important mechanisms affecting the distribution of individuals, populations and communities

51 (Baguette et al. 2013; Lowe and McPeek 2014). At the same time, dispersal is also one of the

52 most difficult phenomena to study even for a single individual or a single species in nature

53 (Bilton et al. 2001; Nathan et al. 2008). The problem is exacerbated for dozens to hundreds of

54 species in a metacommunity, i.e., a set of local communities connected by dispersal (Leibold

55 et al. 2004), making it virtually impossible to account for dispersal directly for such large

56 number of entities in natural settings. Ecologists have therefore relied on various proxies,

57 which are assumed to relate to the effects of dispersal on community structure (Jacobson and

58 Peres-Neto 2010; Jones et al. 2015).

59　　　Dispersal may mask the importance of purely environmental control of local

60 ecological communities (Palmer et al. 1996; Leibold et al. 2004; Brown et al. 2011;

61 Winegardner et al. 2012). This is because very high or very low dispersal rates may interfere

62 with species sorting, decoupling the otherwise strong relationships between biological

63 communities and local environmental factors (Leibold et al. 2004; Ng et al. 2009; Brown and

64 Swan 2010; Winegardner et al. 2012). For instance, in mass effects, very high dispersal from

65 'source' populations may produce a constant flow of migrants that guarantees the

66 maintenance of populations in unsuitable or 'sink' localities (Pulliam 1988), thus interfering

67 with local environmental control (Mouquet and Loreau 2003). On the other hand, species

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

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

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

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

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

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

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

75   2015; Soininen, 2016). An alternative view suggests that statistical models may also

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

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

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

79   dispersal better into account in metacommunity ecology.

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

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

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

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

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

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

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

87   2006; Erős and Campbell Grant 2015). We emphasize that different types of freshwater

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

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

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

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

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

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

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

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

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

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

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

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

100 pristine to impacted sites is high.

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

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

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

104 2001; Grant et al. 2007; Altermatt 2013). It can be assumed that most of the dispersal of

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

123

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

125

126   *The distance effect: "...near things are more related than distant things"*

127

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

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

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

131   2007), it has an inherent emphasis on Euclidean distances between sites. Nature and

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

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

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

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

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

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

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

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

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

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

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

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

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

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

146   1).

147

148   *Organismal-based proxies*

149

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

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

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

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

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

155   2006; Göthe et al. 2013a, 2013b; Grönroos et al. 2013; Heino 2013b; Cañedo-Argüelles et al.

156   2015; Heino et al. 2015a).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

175   without considering dispersal mode.

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

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

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

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

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

181   (2000) also emphasised that wing size allows to identify poor dispersers among groups of

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

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

184   extinction dynamics in metacommunities and consequent applications in environmental

185   research.

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

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

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

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

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

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

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

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

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

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

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

197   assessment contexts.

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

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

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

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

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

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

204

205   *Molecular genetic proxies*

206

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

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

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

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

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

212   2009). These methods also have some drawbacks, such as "detecting" a species when it is not

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

236 2013) that do not consider changes in the environmental conditions in space and assume that

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

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

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

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

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

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

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

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

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

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

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

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

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

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

251

252 *Graph-based proxies*

253

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

270   the patches may be considered unconnected.

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

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

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

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

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

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

277   2004; Dale and Fortin 2010).

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

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

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

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

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

283   2013; Silva and Hernández 2015; Cañedo-Argüelles et al. 2015; Kärnä et al. 2015; Datry et

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

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

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

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

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

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

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

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

292   2007). This is because upstream dispersal is more difficult than downstream dispersal from

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

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

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

296   1).

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

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

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

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

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

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

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

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

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

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

307   ecosystems (Kärnä et al. 2015).

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

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

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

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

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

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

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

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

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

317   Campbell Grant 2015).

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

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

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

321   2011). A problem in the extension of this approach to sets of species is that their dispersal

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

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

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

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

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

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

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

329   their natural history.

16

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

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

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

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

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

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

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

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

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

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

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

341   research in freshwater systems.

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

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

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

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

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

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

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

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

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

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

352   localities in the landscape.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

385   general terms.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

401   biological dissimilarity provides information about the biological connectivity between sites

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

403

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

405

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

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

408   2016) and the terms (Dispers* AND metacommunity*), in the field TOPIC. These terms

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

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

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

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

413   geography proxies in metacommunity ecology.

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

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

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

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

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

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

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

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

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

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

20

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

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

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

427 account in metacommunity studies.

428

429 Statistical approaches to model dispersal influences on biological communities

430

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

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

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

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

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

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

437 2012), and we briefly emphasize that they deserve their place in community ecologists'

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

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

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

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

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

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

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

445 the explanatory variables derived from spatial eigenfunction analysis may overestimate

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

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

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

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

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

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

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

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

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

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

456   Vellend et al. 2014).

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

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

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

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

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

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

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

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

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

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

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

468

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

470

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

501 relevant proxies in various ecosystem types.

502

503 **Applications of proxies for dispersal**

504

505 *Applied research benefitting from use of dispersal proxies*

506

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

534   2001). Hence, rather than restoring only local sites, restoration of connectivity is also a

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

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

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

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

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

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

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

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

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

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

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

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

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

548

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

550

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

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

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

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

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

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

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

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

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

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

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

562   ultimately depend on its ability to reach the site.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

591   of constituent freshwater ecosystems.

592

593   **Questions for further freshwater research**

594

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

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

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

598   proxies in bioassessment, restoration and conservation biology.

599

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

601

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

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

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

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

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

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

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

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

610 landscape.

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

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

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

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

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

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

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

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

619 recognized (Erős and Campbell Grant 2015).

620

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

622

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

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

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

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

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

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

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

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

631 2013a) and/or if species have weak dispersal ability. In this case, we may classify sites in the

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

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

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

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

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

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

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

639   2015).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

655   high dispersal.

656

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

658

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

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

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

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

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

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

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

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

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

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

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

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

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

672

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

674

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

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

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

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

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

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

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

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

683   invasive species (Havel et al. 2005).

684

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

686

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

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

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

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

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

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

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

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

695

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

697

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

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

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

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

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

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

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

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

706   geography proxies might be useful in this context.

707

Where to go from here?

709

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

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

712 conceptual model (e.g. environmental change → local community structure) suggests that a

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

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

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

716 would function as a covariate (e.g. environmental change → local community structure ←

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

732 proxies for dispersal.

733

734 **Conclusions**

735

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

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

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

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

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

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

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

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

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

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

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

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

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

749 considered as tools guiding environmental management and decision making.

750

751 **Acknowledgments**

752

761

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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

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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

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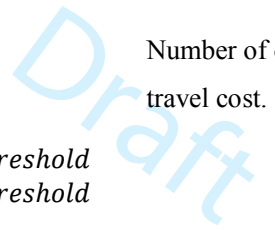|		
	than just topographic characteristics in a landscape. Potentially may be well used to model dispersal routes in heterogeneous landscapes.	calculating more complex cost distances between sites. Also, what, how and when to consider a landscape feature suitable or not suitable for dispersal may be 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

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| 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. |

Draft

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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).

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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

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| 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 | $$P_{ij} = \frac{A_j^\alpha d_{ij}^{-\beta}}{\sum_{j=1}^{n} A_j^\alpha d_{ij}^{-\beta}}$$ | 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.

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** May be an organism, a species, a group of species (i.e. a community), a specific habitat or a biome.

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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. Background map contains data from the National Land Survey of Finland Topographic Database (04/2015) and Elevation model 10 m (04/2015), licensed under a Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/).

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.
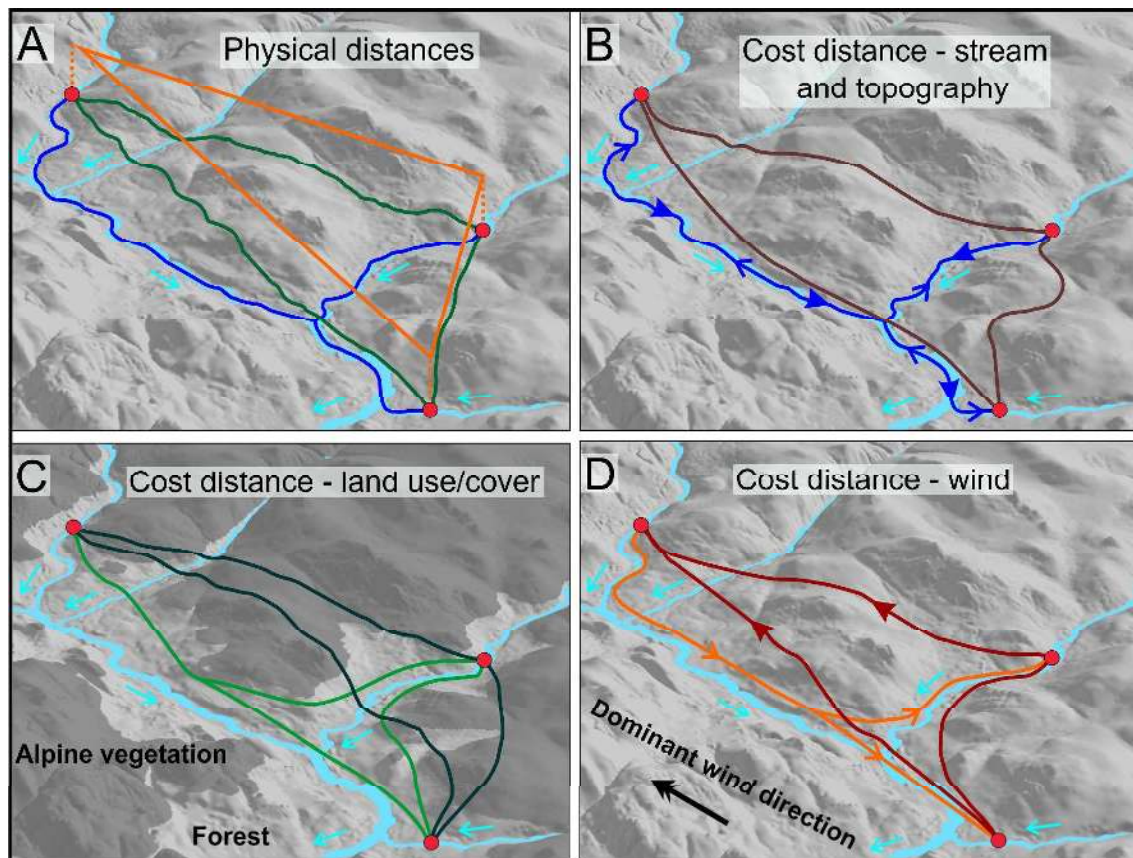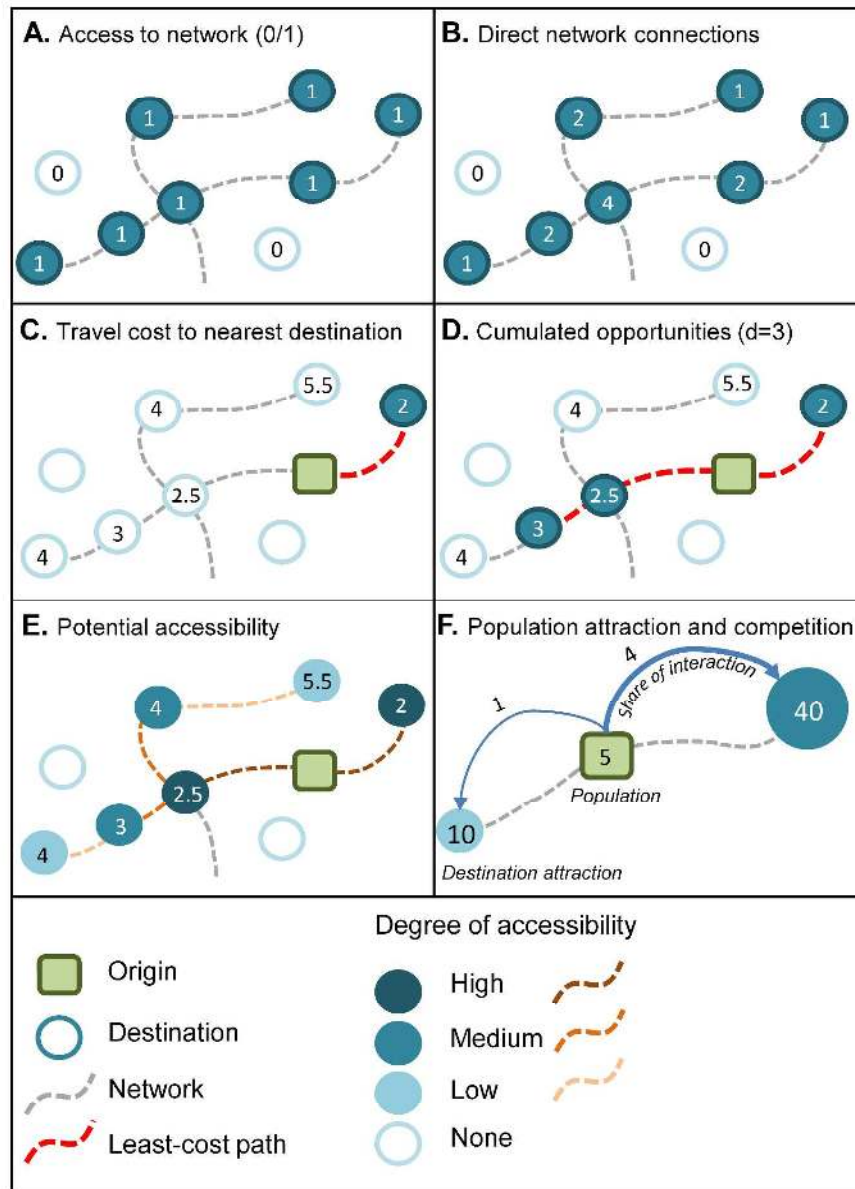
Fig. 1.

Fig. 2.

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Fig. 3.