

1 **What is a macrophyte patch? Patch identification in aquatic** 2 **ecosystems and guidelines for consistent delineation**

3

4 **Abstract**

5 Patches are of central interest to many areas of environmental science because they provide a lower
6 limit of structural detail in synoptic studies, and an upper limit of contextual structure for point
7 measurement-based studies. Identification and delineation of macrophyte patches however, is
8 often arbitrary and case-specific. In this paper we propose a widely-applicable set of guidelines
9 for delineating a “patch” and “patch matrix” – the latter implying a collection of interacting patches
10 – which could standardize future research. To support this proposal, we examine examples from
11 eco-hydrological studies, focusing on interactions between plants, water flow, sediment, and
12 invertebrates. We discuss three aspects that are key to the delineation of a patch: (1) constitution
13 (variable(s) whose values define the patch), (2) extent (patch boundaries), and (3) distinction (of
14 isolated single patches from multiple separate-but-interacting patches). The discussion of these
15 aspects results in guidelines for identifying and delineating a patch which is applicable to any
16 aquatic habitat, and covers a broad range of disciplines such as plant and animal ecology,
17 biogeochemistry, hydraulics, and sedimentology.

18

19 **Keywords:** landscape ecology; pattern identification; plant-flow interaction; spatial scales;
20 ecohydrology; macrophytes

21

22 **Main Text**

23 1. Why do we need these guidelines?

24 Self-organised patch formation is a process whereby large-scale ordered spatial patterns emerge
25 from disordered initial conditions through local interactions between organisms and their
26 environment (Rietkerk & Van de Koppel 2008). This process has recently gained increased
27 scientific attention because it has important implications for ecosystem functioning. Patchiness
28 may be interpreted as an early warning sign of tipping points in ecosystems at which a sudden shift
29 to a contrasting regime may occur (Scheffer et al. 2009). Self-organised patch formation can also
30 increase ecosystem productivity as well as resilience and resistance to global environmental
31 change, compared to spatially homogeneous ecosystems (Rietkerk & Van de Koppel 2008).
32 Patches are also important in facilitating the colonization of initially bare landscapes and their
33 subsequent bio-geomorphic evolution (Gurnell 2014; Vandenbruwaene et al. 2011), and they also
34 have a role in regulating fluxes of water (Rietkerk et al. 2004) and sediments (van Wesenbeeck et
35 al. 2008). Correct delineation of patches is therefore extremely important (Li & Reynolds 1995),
36 especially in multidisciplinary studies where every specialist may define patches differently
37 (O'Hare 2015).

38

39 The term “patch” is commonly used in aquatic ecology to distinguish, for instance: (i) patches of
40 vegetation from surrounding bare areas, e.g. within rivers and lakes (Kleeberg et al. 2010; Naden
41 et al. 2006; Schoelynck et al. 2014; Schoelynck et al. 2012), on river floodplains (Francis et al.
42 2009; Gurnell 2014), in riparian wetlands (Opdekamp et al. 2012), or on intertidal floodplains
43 (Bouma et al. 2009; Bouma et al. 2013; Bouma et al. 2007; Vandenbruwaene et al. 2011), (ii)
44 diatom aggregations from bare tidal mudflats (Weerman et al. 2012); (iii) zones with fine sediment
45 from zones with coarser grain sizes (Gibbins et al. 2007); (iv) nutrient-rich from nutrient-poor
46 zones (Hodge 2004; Hutchings & Wijesinghe 2008); (v) zones of high hydrodynamic stress from

47 more quiescent zones (Lancaster & Hildrew 1993); (vi) coral reefs from sea grass beds (Maldonado
48 et al. 2010); (vii) food-rich from food-depleted locations (Thums et al. 2013), (viii) zones of high
49 variability in populations of soil organisms from zones with less variability (Ettema & Wardle
50 2002) and even (ix) areas modified by ecosystem engineers (Wright et al. 2002), from areas not
51 modified in this way. The implication common to all of these examples (and the many others in
52 which the term is used (Townsend 1989)) is that patches are areas characterised by values of a
53 parameter of interest that are relatively high or low compared to the mean value across the whole
54 area being studied. As such, patches tend to be viewed in two ways. Firstly, in synoptic scale
55 studies, they are identified as the lower limit of structural detail, for example where a landscape is
56 characterised in terms of the size and shape statistics of patches of a certain kind of habitat (e.g.
57 Visser et al. (2015), who used low-altitude imaging to map submerged aquatic vegetation patches).
58 Secondly, in studies executed via point measurements, they are identified as the upper limit of
59 contextual structure, for example where comparisons are made between measurements within and
60 outside of patches. Thus, a patch has a finite spatial extent (distinguishing it from a “point”) but is
61 smaller than the entire study area.

62

63 2. Examples of macrophyte patches in aquatic environments

64 In some cases, macrophyte patches are easily and rather unambiguously defined, whereas in many
65 other situations, especially in aquatic habitats, the delineation of patches is less straightforward
66 (Kolasa 2014). For example: plant patches identified in aquatic environments can be categorised
67 into four groups. In the first category, plant patches are easily recognised (Figure 1a). These consist
68 of a single species at a relatively high density within patches whose edges are sharp. This category
69 appears especially in subaqueous systems (Figure 1b). It is also frequently found on mudflats

70 where patches of pioneer plants are formed by the establishment of a few individual plants that
71 then expand clonally (Figure 1c). In the second category (Figure 1d), patches still consist of a
72 single species, but the edges are less sharp because the density of shoots does not change quasi-
73 discontinuously as in the first category; instead the patch fades into areas better identified as
74 collections of isolated individual shoots. This configuration is often found in subaqueous systems
75 where a group of individuals emerges from a seed bank (Figure 1e), and can also occur at the edges
76 of lakes or marshes (Figure 1f). In the third category (Figure 1g), patches consist of two or more
77 species. This is common in subaqueous systems where single shoots of different species grow in
78 amongst each other, or where stands of different species are interwoven (Figure 1h). Finally, in
79 the fourth category (Figure 1i), two or more patches of the same or of different species grow
80 separately, but interact with each other in such a way that they can be regarded as one under certain
81 circumstances (see later). This category is frequently found in the field (e.g. Figure 1j), and
82 includes situations where it is difficult to demarcate the outer edges of the region of the patches'
83 mutual interaction with the flow of water, and hence its size. From these four categories, we
84 identify three characteristics of patches which will form the basis of our guidelines: (a) their
85 **constitution** – i.e. the variable(s) whose values define the patch; (b) their **extent** – i.e.
86 identification of patch boundaries; and (c) their **distinction** – i.e. distinguishing multiple separate-
87 but-interacting patches from single patches.

88

89 Because patch identification and consistent delineation is very often ambiguous, calculating
90 statistics of patch size and shape can be problematic, and can cause difficulties with determining
91 whether measurement points are truly within or outside of patches. The intention of this paper,
92 therefore, is to review situations in which patches are identified in aquatic environments and

93 provide a clear and widely-applicable set of guidelines for defining the term “patch” using the
94 three identified patch characteristics. This will enable researchers a standardised way of comparing
95 different studies that use this term, or comparing studies that use field measurements, laboratory
96 experiments or numerical models.

97

98 3. Guidelines for defining a patch

99 *Guideline 1: define the constitution of the patch*

100 We illustrate the issues that may cause problems or ambiguities in relation to this characteristic of
101 patches with an example of the relationships between aquatic plants, water flow, sediment and
102 macroinvertebrates. Sand-Jensen (1998) demonstrated the entrapment of fine sediment by mono-
103 specific patches of submerged macrophytes in rivers due to their reduction of the near-bed flow
104 velocity. Gibbins et al. (2007) concluded that, in this context, hydrological disturbance can
105 influence benthic invertebrate density distribution, because the high erodibility of the fine sediment
106 patches causes entrainment of benthic invertebrates from the patches into the flow. The size of the
107 macrophyte patch, however, does not need to correspond exactly to the size of the habitat with
108 similar substrate conditions for benthic macroinvertebrate species: the latter may extend upstream
109 and downstream of the macrophytes because of wakes, or be fragmented due to local erosion
110 within the macrophyte patch itself. So, in this situation, the “patch” has a different shape depending
111 on whether it is defined in terms of the macrophytes, the sediment or the benthic macroinvertebrate
112 habitat.

113

114 It is clear from this examples that researchers need to state explicitly the variables they use to
115 define a patch. As a result, we cannot simply talk about “patches” but need instead to use a
116 qualifying prefix which identifies the measurement variable. They also imply a need for clear

117 thinking about the research questions or hypotheses that provide the motivation for studies. For
118 instance, consider a researcher who wishes to compare the species richness of the
119 macroinvertebrate community in an area of a river colonised by macrophytes to the community
120 elsewhere in the same river. The sampling locations need to be determined according to whether
121 the question being asked is about the effect of the macrophytes in forming regions of low
122 hydrodynamic energy, or the direct effect of the plants (e.g. as physical anchorage sites)
123 themselves. In the former case, the ‘patch’ needs to be defined by hydrodynamic parameters; in
124 the latter case, it needs to be defined by macrophyte density. *Thus, our guideline in terms of this*
125 *first characteristic of patches requires structuring research questions or hypotheses and sampling*
126 *strategies, and identifying the appropriate parameter for defining the patch accordingly.*

127

128 *Guideline 2: define the extent of the patch*

129 This spatial characteristic of patches is problematic because without agreement on it there is no
130 clear way of defining where patches begin and end. This can be a problem for studies that wish to
131 compare parameters in- and outside patches, although in many cases these take point
132 measurements at locations that are unequivocally in- or outside a patch. However, where mean or
133 total values of parameters across patches are required, for example when measuring nutrient
134 stocks, knowing where the edge of a patch occurs is crucial. Moreover, in synoptic scale studies,
135 interest is often focused on parameters such as patch size, shape, perimeter length etc. In these
136 cases, clear definition of patches is absolutely required.

137

138 Problems of patch edge definition also arise when we want to translate laboratory or numerical
139 model results into field contexts or vice versa, because the patches in experiments or models may
140 be different in this sense from the real patches in the field. Patches in models or experiments tend

141 to have constant densities and quasi-discontinuous edges. In the field however, patches rarely have
142 either of these characteristics: density (of whatever variable defines their constitution) varies
143 within them, and fades out gradually and three-dimensionally. This can lead to inconsistent
144 definitions of patch edges. But experimental results can imply a need to delineate patches in a
145 concise and objective way. For example, Morris et al. (2008) and Bal et al. (2013) each reported a
146 laboratory flume experiment studying spatially-explicit ammonia uptake rates in the presence of
147 homogeneous, sharp-edged seagrass and river macrophyte patches, respectively. Both found that
148 these uptake rates were highest at the patch edges. Therefore, estimation of the impact of natural
149 vegetation on nutrient cycling relies on the ability to delineate patches in the field in the same way
150 as both research teams did in their flume. This is an illustration of the fact that, without an objective
151 approach to defining patch edges, the translation of experimental results to field situations is
152 complicated.

153
154 To address this issue, we now provide a practical guideline for defining and delineating patches.
155 We first identify relevant scales that contextualise our definition. At the upper end, the “domain”
156 scale is the scale of the entire region of interest – for example, the experimental section of a
157 laboratory facility or mesocosm, the entire domain of a numerical model, or the field site in which
158 we are working. At the lower end, the “individual element” scale is the smallest scale of objects
159 we are focusing on - for example, single shoots if we are studying vegetation, or single sediment
160 particles if we are studying bed material. The “measurement” scale depends on the mode of
161 measurement and consists of a resolution and a footprint. The resolution is the density of
162 measurement points within the domain (e.g. the number of sediment cores per transect). The
163 footprint is the area covered by the measurement point (e.g. the cross-sectional area of the corer).
164 We assume that the measurement scale (both resolution and footprint) is coarser than the individual

165 element scale, thus enabling meaningful measurement of the density of individual elements. If this
166 is not the case, we would not define the observed distribution to be patchy, but as being made up
167 of isolated individual elements.

168

169 We define the patch scale to be smaller than the domain scale, but larger than the individual
170 element scale and measurement scales. Thus, patches are distinguished from both individual
171 elements and phenomena that are homogeneous at the domain scale. We illustrate our method for
172 delineating a patch using a simple example (Figure 2). We first identify a point where the variable
173 under consideration has a local maximum, and thus is unequivocally located inside the patch. We
174 then project an array of radial lines emanating from that point. We then identify a local minimum
175 of the variable under consideration on each line, such that all of these local minima are co-
176 contiguous. For example, if there is a small gap within a macrophyte patch, the minimum in shoot
177 density within that gap is not contiguous with the minima in shoot density around the patch, and
178 only the latter ones will be considered. Along each radial, we then select the point between the
179 local maximum and the first local minimum at which the gradient in our variable of interest is
180 greatest. Finally, if these all are co-contiguous, we join up all of these maximum-gradient points
181 to create the patch boundary. Note that in cases where patches consist of low values compared to
182 the surroundings (e.g. flow velocities in a wake), then the terms minimum and maximum in this
183 description would need to be switched.

184

185 *Thus, our guideline in terms of this second characteristic of patches enables distinction between*
186 *the spatial extent of patches of different constitutions (in the sense defined above) using practical*
187 *steps for defining and delineating patches.* Note also that in cases where two regions of high plant
188 density are separated by a region in which the plant density is slightly lower, such that the flow

189 skims unaltered over both the patches and the region between them, this method would identify
190 two vegetation patches, but only one hydrodynamic patch.

191
192 Clearly, deployment of this guideline for patch delineation will differ depending on the context. In
193 numerical models, and many laboratory flume setups, it can be used objectively and precisely, and
194 may well be trivial. In the field, however, because of the increased complexity of the setting, an
195 objective and precise approach might involve unnecessary time and costs, and we envisage that
196 our guidelines' use would be guided by expert, but subjective, judgment. Nevertheless, modern
197 techniques allow to acquire detailed information about in-stream plant patch sizes and distribution
198 by digital cover photography (Verschoren et al. 2017), or flow fields through particle imaging
199 velocimetry (Creëlle et al. in press).

200

201 *Guideline 3: define the distinction or interaction between patches*

202 The patch characteristics that have been defined so far are appropriate for individual patches.
203 Patches of organisms may however, have an influence on their surrounding environment, i.e.
204 beyond the patch edges. For example, vegetation patches in aquatic environments influence flow
205 velocities and sediment deposition next to and behind the patches (wakes); allelopathic interactions
206 between *Stratiotes aloides* and filamentous algae and competition for nutrients cause gaps in the
207 algae mats surrounding the plants (Mulderij et al. 2009); patches (i.e. *tussocks*) of riparian wetland
208 plants influence their environment by shading (Opdekamp et al. 2012; van de Koppel & Crain
209 2006). We define circumstances where the zones of patches' influence overlap of each other as
210 interaction between patches. Furthermore, we define cases where multiple patches interact in some
211 way and thus form a different, larger spatial structure as "patch matrices" (see e.g. (Turner et al.
212 2001; Wagner & Fortin 2005), and we need to distinguish matrices of interacting patches from

213 both isolated patches, and phenomena that are homogeneous at the domain scale. *Our guideline in*
214 *terms of this third characteristic of patches requires a combination of the information of all*
215 *parameters in question and detect if any relevant interaction exists among them.* It is illustrated
216 with three distinct situations, in each of which two variables – occurrence of aquatic vegetation
217 and flow field characteristics – are discussed (Figure 3).

218
219 In Figure 3a, the areas of vegetation are well-separated from each other. Thus, it is appropriate to
220 consider each of these areas as an individual patch of vegetation. In this scenario, all of the
221 hydrodynamic wakes are also independent as the occurrence of one wake has no influence on any
222 other wake. Each wake is therefore an individual hydrodynamic patch. In Figures 3b and 3c,
223 despite the vegetation patches being closer together, there is still space in between them. Hence,
224 using the patch delineation guidelines proposed above, the vegetation can still be defined as a
225 cluster of distinct vegetation patches. However, this is not the case for the hydrodynamic wakes as
226 they now merge with each other and cannot be considered spatially separated. Figure 3b shows the
227 clearest form of interaction. Here the individual wakes are not indistinguishable at the
228 measurement scale and become one large wake, i.e. one large hydrodynamic patch. In Figure 3c,
229 the intermediate situation between Figures 3a and 3b is depicted. Here, the wakes are distinct
230 upstream, but subsequently merge to a certain extent downstream. We define this case, where the
231 vegetation patches are distinct, but their hydrodynamic influence zones are not, as a
232 “hydrodynamic patch-matrix” or “a matrix of hydrodynamic patches”. We must distinguish (e.g.
233 for the purposes of sampling or modelling) between the region of several individual hydrodynamic
234 patches (wakes) and the region of one merged hydrodynamic patch. Matrices of patches are made
235 up of distinct patches which nevertheless interact in some way. These distinctions can be seen as
236 analogous to those between ‘isolated roughness flow’ (c.f. Figure 3a), ‘skimming flow’ (c.f. Figure

237 3b) and ‘wake interference flow’ (Figure 3c), which were first proposed in the engineering
238 literature (Morris 1955) and which have been adopted in the ecohydrology literature more recently
239 (Davis & Barmuta 1989; Folkard 2011; Young 1992).

240

241 These different levels of interaction are illustrated by Sukhodolova (2008) and Sukhodolov and
242 Sukhodolova (2010), who studied the effect of different distributions of submerged vegetation (at
243 different times in the annual growth cycle in the same river reach) on turbulent flow structure in a
244 lowland river. Variation in the extent of 233 vegetation patches over the growing season changed
245 the interaction between the hydrodynamic wakes. In the summer cases there was relatively little
246 separation between the patches, producing one combined hydrodynamic wake patch (c.f. Figure
247 3b). In the early spring situations, when the vegetation was less developed, individual vegetation
248 patches producing individual hydrodynamic patches were observed (c.f. Figure 3a). Finally, at
249 intermediate vegetation patch separation, the individual vegetation patches produced
250 hydrodynamic patches which were at first distinct but subsequently merged, i.e. a hydrodynamic
251 patch matrix (c.f. Figure 3c). Another example of how systems can move from one of these
252 configurations to the others over time is provided by Vandenbruwaene et al. (2011), who
253 investigated the evolution of a tidal landscape undergoing colonisation by vegetation patches that
254 are laterally expanding in size and therefore grow closer to each other. Initially, the situation they
255 observed corresponded with Figure 3a, where the vegetation formed non-interacting patches (see
256 also Figure 1c). As the vegetation patches grew bigger and closer to each other, the high level of
257 influence between the hydrodynamic wakes made it impossible to define isolated hydrodynamic
258 patches, hence they moved first to the situation in Figure 3c, and ultimately to that in Figure 3b.

259

260 The often complex interactions between vegetation, fauna, hydrodynamics and sedimentary
261 processes that are studied in multidisciplinary studies imply that changes in any one of them can
262 alter the patch/patch-matrix structure in the others. Careful patch definition is particularly
263 important in measuring and modelling this kind of multi-faceted situation (Marion et al. 2014). An
264 example of this is provided in Figure 4.

265

266 4. Outlook

267 We now revisit the examples presented in Figure 1 and apply the 3 guidelines we have defined in
268 Section 3 to each of them. The Category I examples (Figures 1b and 1c) show patches whose
269 constitution is defined by vegetation shoot density, whose extents are defined by sharp edges, and
270 which are individual patches in a shoot-density sense, but which may form inter-connected
271 matrices in terms of hydrodynamic, sedimentary conditions, macroinvertebrate communities
272 and/or substrate nutrient distributions. If these individual patches grow, they will move from
273 patches that are isolated in every sense (c.f. Figure 3a) to interacting matrices of individual patches
274 (c.f. Figure 3c, then Figure 3b) to single, merged patches. Thus, while the delineation of the
275 vegetation patches, for example for the purposes of measuring their size and shape, is relatively
276 unambiguous, their sampling for macroinvertebrate, sediment or hydrodynamic parameters
277 requires careful consideration of the extent to which they form a matrix in these terms. Moreover,
278 understanding the role they play in affecting hydrodynamic, sedimentary or macroinvertebrate
279 conditions requires an appreciation of their matrix-scale interactions.

280

281 The Category II examples (Figures 1e and 1f) show patches defined again by vegetation shoot
282 density. How to delineate them is less clear than for Category I cases, but the guideline defined in
283 Section 3b provides an unambiguous way of achieving this. Interactions between patches in

284 situations such as these are likely to be enhanced by the presence of regions of lower vegetation
285 density between defined patches, and thus matrix-scale structures are likely to be more important
286 here than in Category I cases.

287

288 The Category III case shown in Figure 1h contains what may be considered to be a single
289 vegetation patch, or a series of separate patches of different vegetation species, depending on how
290 the constitution of the patches is defined. Macroinvertebrate, sedimentary and hydrodynamic
291 parameter patch configuration in these conditions may be similar or different between the patches
292 of different species depending on the similarity or difference of the plants' morphologies and their
293 interactions with these parameters. As with Category II, although the extent of each patch may
294 appear difficult to define at first sight, the guidelines we provide give a clear way of identifying
295 the edge of each patch, depending on the parameter that defines it.

296

297 Finally, the Category IV example shown in Figure 1j can be clearly described in terms of the
298 guidelines for investigating patch interactions (Section 3c) as two vegetation patches and one
299 hydrodynamic patch matrix (with flow direction, visualised by the tracers shown, as the
300 hydrodynamic parameter under consideration). These are also likely to have merged, matrix-scale
301 configurations of sediment and macroinvertebrate communities.

302

303 Thus, our guidelines of patch and matrix-scales provide a comparative framework within which
304 understanding of these disparate contexts can be brought together. They also imply the need for
305 further numerical and laboratory modelling efforts. Investigations are required of the matrix-scale
306 connectivity of patches in terms of the wide variety of variables considered above. Studies of the
307 effects of gradual changes in parameters such as shoot density, rather than the sharp-edged patch

308 configurations that have heretofore been used in physical and numerical modelling studies are
309 required. Studies of mixed patches (for example, patches made up of more than one
310 species/morphology of vegetation) are also virtually non-existent in the literature and require
311 attention. In some cases, absolute-value thresholds might be appropriate (e.g. a fixed altitude to
312 delineate bathymetry), while boundaries defined by gradient-maxima, absolute gradient values or
313 other measures might be more appropriate in other situations. This variety of threshold definitions
314 can be easily accommodated within GIS-software packages. Once patches are defined, other
315 software can be used to analyse them (e.g. Fragstats).

316

317 In conclusion: we provided a relatively rigid method to approach the identification and delineation
318 of patches and patch-matrices, which also serves as a platform for consistency across studies. We
319 have provided a framework that can give consistent guidance in situations where patch definition
320 may be ambiguous. Our intention is that, as well as providing a framework within which studies
321 from different environmental contexts can be meaningfully compared and mutually enhanced, the
322 definitions and guidelines proposed here also provide a means for strengthening the mutual support
323 of field, physical and numerical modelling studies of complex interacting systems such as those
324 considered in this paper.

325

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328

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441 **Figure captions**

442 **Figure 1.** Examples of different vegetation patch categories. White arrows indicate mean flow
443 direction. (a) Category I, well-delineated, single species patches, e.g. (b) *Ranunculus sp.* in a river;
444 (c) Cord-grass [*Spartina anglica*] on tidal mudflats. (d) Category II, single species patches, poorly
445 delineated (circles represent single shoots), e.g. (e) Bur-reed [*Sparganium emersum*] in a river; (f)
446 Bulrush [*Typha latifolia*] by a lake. (g) Category III, multiple species growing together, e.g. (h) at
447 least five different submerged species in a river. (i) Category IV, delineated vegetation patches
448 acting hydrodynamically as one, e.g. (j) two reed canary grass patches [*Phalaris arundinacea*]
449 with a combined effect on the flow (visualised by white tracers).

450 **Figure 2.** Definition diagram for patch edge identification method. Panel (a) shows the side view
451 of the spatial distribution of vegetation. The vegetation on the left side is quite straightforward to
452 identify as a patch, but the cluster of vegetation on the right side is somewhat ambiguous. To
453 determine the patch edges, we choose the local maximum within each patch (yellow line in panel
454 a, yellow dot in panel c), and draw radial lines in all directions (black dashed lines, panel c). The
455 points where the change of the variable of interest (panel b) is at its maximum (vertical grey dashed
456 lines) are joined up to create the patch boundary (panel c). As a result, we have now identified and
457 delineated three distinct patches following the same guidelines.

458

459 **Figure 3.** Guideline diagram to distinguish individual patches from patch matrices. Blue arrows
460 indicate the angle of attack of the incoming flow. Panel (a) shows 10 distinct vegetation patches
461 (green circles) and 10 distinct hydrodynamic patches (grey triangles). Panel (b) shows 10
462 individual vegetation patches and 1 hydrodynamic patch (dark grey triangle). Panel (c) shows 10
463 distinct vegetation patches and 1 hydrodynamic patch matrix because the different hydrodynamic
464 wake zones interact.

465 **Figure 4.** (a) Plan view sketch illustrating interactions between vegetation, hydrodynamic,
466 macroinvertebrate and erosion patches. Blue arrows show flow direction; green circles indicate
467 macrophyte patches; grey triangles indicate hydrodynamic patches (wakes) according to figure 3b;
468 black areas indicate erosion patches (scour zones); black dashed lines indicate patches of low-flow
469 favouring limnophilic macroinvertebrates such as *Asselus aquaticus*; white dashed lines indicate
470 patches of high-flow favouring rheophilic macroinvertebrates such as *Rhitrogena germanica*. (b)
471 Higher flow has a negative effect on the connectivity of the low-flow macroinvertebrates, but may
472 cause stronger merging of the erosion patches with a positive effect on the connectivity of high-
473 flow macroinvertebrates.