

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

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32 **Keywords**

33 Landscape ecology; Pattern identification; Plant-flow interaction; Spatial scales; Ecohydrology;
34 Macrophytes

35

36 **Abstract**

37 Patches are of central interest to many areas of environmental science because they provide a lower
38 limit of structural detail in synoptic studies, and an upper limit of contextual structure for point
39 measurement-based studies. Identification and delineation of macrophyte patches however, is
40 often arbitrary and case-specific. In this paper we propose a widely-applicable set of guidelines
41 for delineating a “patch” and “patch matrix” – the latter implying a collection of interacting patches
42 – which could standardize future research. To support this proposal, we examine examples from
43 eco-hydrological studies, focusing on interactions between plants, water flow, sediment, and
44 invertebrates. We discuss three aspects that are key to the delineation of a patch: (1) constitution
45 (variable(s) whose values define the patch), (2) spatial properties (patch boundaries), and (3)
46 distinction (of isolated single patches from multiple separate-but-interacting patches). The
47 discussion of these aspects results in guidelines for identifying and delineating a patch which is

48 applicable to any aquatic habitat, and covers a broad range of disciplines such as plant and animal
49 ecology, biogeochemistry, hydraulics, and sedimentology.

50

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

53

54 **Main Text**

55 1. Why do we need these guidelines?

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

70

71 The term “patch” is commonly used in aquatic ecology to distinguish, for instance: (i) patches of
72 vegetation from surrounding bare areas, e.g. within rivers and lakes (Kleeberg et al. 2010; Naden
73 et al. 2006; Schoelynck et al. 2014; Schoelynck et al. 2012), on river floodplains (Francis et al.
74 2009; Gurnell 2014), in riparian wetlands (Opdekamp et al. 2012), or on intertidal floodplains
75 (Bouma et al. 2009; Bouma et al. 2013; Bouma et al. 2007; Vandenbruwaene et al. 2011), (ii)
76 diatom aggregations from bare tidal mudflats (Weerman et al. 2012); (iii) zones with fine sediment
77 from zones with coarser grain sizes (Gibbins et al. 2007); (iv) nutrient-rich from nutrient-poor
78 zones (Hodge 2004; Hutchings & Wijesinghe 2008); (v) zones of high hydrodynamic stress from
79 more quiescent zones (Lancaster & Hildrew 1993); (vi) coral reefs from sea grass beds (Maldonado
80 et al. 2010); (vii) food-rich from food-depleted locations (Thums et al. 2013), (viii) zones of high
81 variability in populations of soil organisms from zones with less variability (Ettema & Wardle
82 2002) and even (ix) areas modified by ecosystem engineers (Wright et al. 2002), from areas not
83 modified in this way. The implication common to all of these examples (and the many others in
84 which the term is used (Townsend 1989)) is that patches are areas characterised by values of a
85 parameter of interest that are relatively high or low compared to the mean value across the whole
86 area being studied. As such, patches tend to be viewed in two ways. Firstly, in synoptic scale
87 studies, they are identified as the lower limit of structural detail, for example where a landscape is
88 characterised in terms of the size and shape statistics of patches of a certain kind of habitat (e.g.
89 Visser et al. (2015), who used low-altitude imaging to map submerged aquatic vegetation patches).
90 Secondly, in studies executed via point measurements, they are identified as the upper limit of
91 contextual structure, for example where comparisons are made between measurements within and
92 outside of patches. Thus, a patch has a finite spatial extent (distinguishing it from a “point”) but is
93 smaller than the entire study area.

94

95 2. Examples of macrophyte patches in aquatic environments

96 In some cases, macrophyte patches are easily and rather unambiguously defined, whereas in many
97 other situations, especially in aquatic habitats, the delineation of patches is less straightforward
98 (Kolasa 2014). For example: plant patches identified in aquatic environments can be categorised
99 into four groups. In the first category, plant patches are easily recognised (Figure 1a). These consist
100 of a single species at a relatively high density within patches whose edges are sharp. This category
101 appears especially in subaqueous systems (Figure 1b). It is also frequently found on mudflats
102 where patches of pioneer plants are formed by the establishment of a few individual plants that
103 then expand clonally (Figure 1c). In the second category (Figure 1d), patches still consist of a
104 single species, but the edges are less sharp because the density of shoots does not change quasi-
105 discontinuously as in the first category; instead the patch fades into areas better identified as
106 collections of isolated individual shoots. This configuration is often found in subaqueous systems
107 where a group of individuals emerges from a seed bank (Figure 1e), and can also occur at the edges
108 of lakes or marshes (Figure 1f). In the third category (Figure 1g), patches consist of two or more
109 species. This is common in subaqueous systems where single shoots of different species grow in
110 amongst each other, or where stands of different species are interwoven (Figure 1h). Finally, in
111 the fourth category (Figure 1i), two or more patches of the same or of different species grow
112 separately, but interact with each other in such a way that they can be regarded as one under certain
113 circumstances (see later). This category is frequently found in the field (e.g. Figure 1j), and
114 includes situations where it is difficult to demarcate the outer edges of the region of the patches'
115 mutual interaction with the flow of water, and hence its size. From these four categories, we
116 identify three characteristics of patches which will form the basis of our guidelines: (a) their

117 **constitution** – i.e. the variable(s) whose values define the patch; (b) their **extent** – i.e.
118 identification of patch boundaries; and (c) their **distinction** – i.e. distinguishing multiple separate-
119 but-interacting patches from single patches.

120

121 Because patch identification and consistent delineation is very often ambiguous, calculating
122 statistics of patch size and shape can be problematic, and can cause difficulties with determining
123 whether measurement points are truly within or outside of patches. The intention of this paper,
124 therefore, is to review situations in which patches are identified in aquatic environments and
125 provide a clear and widely-applicable set of guidelines for defining the term “patch” using the
126 three identified patch characteristics. This will enable researchers a standardised way of comparing
127 different studies that use this term, or comparing studies that use field measurements, laboratory
128 experiments or numerical models.

129

130 3. Guidelines for defining a patch

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

132 We illustrate the issues that may cause problems or ambiguities in relation to this characteristic of
133 patches with an example of the relationships between aquatic plants, water flow, sediment and
134 macroinvertebrates. Sand-Jensen (1998) demonstrated the entrapment of fine sediment by mono-
135 specific patches of submerged macrophytes in rivers due to their reduction of the near-bed flow
136 velocity. Gibbins et al. (2007) concluded that, in this context, hydrological disturbance can
137 influence benthic invertebrate density distribution, because the high erodibility of the fine sediment
138 patches causes entrainment of benthic invertebrates from the patches into the flow. The size of the
139 macrophyte patch, however, does not need to correspond exactly to the size of the habitat with
140 similar substrate conditions for benthic macroinvertebrate species: the latter may extend upstream

141 and downstream of the macrophytes because of wakes, or be fragmented due to local erosion
142 within the macrophyte patch itself. So, in this situation, the “patch” has a different shape depending
143 on whether it is defined in terms of the macrophytes, the sediment or the benthic macroinvertebrate
144 habitat.

145

146 It is clear from this examples that researchers need to state explicitly the variables they use to
147 define a patch. As a result, we cannot simply talk about “patches” but need instead to use a
148 qualifying prefix which identifies the measurement variable. They also imply a need for clear
149 thinking about the research questions or hypotheses that provide the motivation for studies. For
150 instance, consider a researcher who wishes to compare the species richness of the
151 macroinvertebrate community in an area of a river colonised by macrophytes to the community
152 elsewhere in the same river. The sampling locations need to be determined according to whether
153 the question being asked is about the effect of the macrophytes in forming regions of low
154 hydrodynamic energy, or the direct effect of the plants (e.g. as physical anchorage sites)
155 themselves. In the former case, the ‘patch’ needs to be defined by hydrodynamic parameters; in
156 the latter case, it needs to be defined by macrophyte density. *Thus, our guideline in terms of this*
157 *first characteristic of patches requires structuring research questions or hypotheses and sampling*
158 *strategies, and identifying the appropriate parameter for defining the patch accordingly.*

159

160 *Guideline 2: define the spatial properties of the patch*

161 These spatial properties of patches is problematic because without agreement on it there is no clear
162 way of defining where patches begin and end. This can be a problem for studies that wish to
163 compare parameters in- and outside patches, although in many cases these take point
164 measurements at locations that are unequivocally in- or outside a patch. However, where mean or

165 total values of parameters across patches are required, for example when measuring nutrient
166 stocks, knowing where the edge of a patch occurs is crucial. Moreover, in synoptic scale studies,
167 interest is often focused on parameters such as patch size, shape, perimeter length etc. In these
168 cases, clear definition of patches is absolutely required.

169

170 Problems of patch edge definition also arise when we want to translate laboratory or numerical
171 model results into field contexts or vice versa, because the patches in experiments or models may
172 be different in this sense from the real patches in the field. Patches in models or experiments tend
173 to have constant densities and quasi-discontinuous edges. In the field however, patches rarely have
174 either of these characteristics: density (of whatever variable defines their constitution) varies
175 within them, and fades out gradually and three-dimensionally. This can lead to inconsistent
176 definitions of patch edges. But experimental results can imply a need to delineate patches in a
177 concise and objective way. For example, Morris et al. (2008) and Bal et al. (2013) each reported a
178 laboratory flume experiment studying spatially-explicit ammonia uptake rates in the presence of
179 homogeneous, sharp-edged seagrass and river macrophyte patches, respectively. Both found that
180 these uptake rates were highest at the patch edges. Therefore, estimation of the impact of natural
181 vegetation on nutrient cycling relies on the ability to delineate patches in the field in the same way
182 as both research teams did in their flume. This is an illustration of the fact that, without an objective
183 approach to defining patch edges, the translation of experimental results to field situations is
184 complicated.

185

186 To address this issue, we now provide a practical guideline for defining and delineating patches.
187 We first identify relevant scales that contextualise our definition. At the upper end, the “domain”
188 scale is the scale of the entire region of interest – for example, the experimental section of a

189 laboratory facility or mesocosm, the entire domain of a numerical model, or the field site in which
190 we are working. At the lower end, the “individual element” scale is the smallest scale of objects
191 we are focusing on - for example, single shoots if we are studying vegetation, or single sediment
192 particles if we are studying bed material. The “measurement” scale depends on the mode of
193 measurement and consists of a resolution and a footprint. The resolution is the density of
194 measurement points within the domain (e.g. the number of sediment cores per transect). The
195 footprint is the area covered by the measurement point (e.g. the cross-sectional area of the corer).
196 We assume that the measurement scale (both resolution and footprint) is coarser than the individual
197 element scale, thus enabling meaningful measurement of the density of individual elements. If this
198 is not the case, we would not define the observed distribution to be patchy, but as being made up
199 of isolated individual elements.

200

201 We define the patch scale to be smaller than the domain scale, but larger than the individual
202 element scale and measurement scales. Thus, patches are distinguished from both individual
203 elements and phenomena that are homogeneous at the domain scale. We illustrate our method for
204 delineating a patch using a simple example (Figure 2). We first identify a point where the variable
205 under consideration has a local maximum, and thus is unequivocally located inside the patch. We
206 then project an array of radial lines emanating from that point. We then identify a local minimum
207 of the variable under consideration on each line, such that all of these local minima are co-
208 contiguous. For example, if there is a small gap within a macrophyte patch, the minimum in shoot
209 density within that gap is not contiguous with the minima in shoot density around the patch, and
210 only the latter ones will be considered. Along each radial, we then select the point between the
211 local maximum and the first local minimum at which the gradient in our variable of interest is
212 greatest. Finally, if these all are co-contiguous, we join up all of these maximum-gradient points

213 to create the patch boundary. Note that in cases where patches consist of low values compared to
214 the surroundings (e.g. flow velocities in a wake), then the terms minimum and maximum in this
215 description would need to be switched.

216

217 *Thus, our guideline in terms of this second characteristic of patches enables distinction between*
218 *the spatial properties of patches of different constitutions (in the sense defined above) using*
219 *practical steps for defining and delineating patches.* Note also that in cases where two regions of
220 high plant density are separated by a region in which the plant density is slightly lower, such that
221 the flow skims unaltered over both the patches and the region between them, this method would
222 identify two vegetation patches, but only one hydrodynamic patch.

223

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

232

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

234 The patch characteristics that have been defined so far are appropriate for individual patches.
235 Patches of organisms may however, have an influence on their surrounding environment, i.e.
236 beyond the patch edges. For example, vegetation patches in aquatic environments influence flow

237 velocities and sediment deposition next to and behind the patches (wakes); allelopathic interactions
238 between *Stratiotes aloides* and filamentous algae and competition for nutrients cause gaps in the
239 algae mats surrounding the plants (Mulderij et al. 2009); patches (i.e. *tussocks*) of riparian wetland
240 plants influence their environment by shading (Opdekamp et al. 2012; van de Koppel & Crain
241 2006). We define circumstances where the zones of patches' influence overlap of each other as
242 interaction between patches. Furthermore, we define cases where multiple patches interact in some
243 way and thus form a different, larger spatial structure as “patch matrices” (see e.g. (Turner et al.
244 2001; Wagner & Fortin 2005), and we need to distinguish matrices of interacting patches from
245 both isolated patches, and phenomena that are homogeneous at the domain scale. *Our guideline in*
246 *terms of this third characteristic of patches requires a combination of the information of all*
247 *parameters in question and detect if any relevant interaction exists among them.* It is illustrated
248 with three distinct situations, in each of which two variables – occurrence of aquatic vegetation
249 and flow field characteristics – are discussed (Figure 3).

250
251 In Figure 3a, the areas of vegetation are well-separated from each other. Thus, it is appropriate to
252 consider each of these areas as an individual patch of vegetation. In this scenario, all of the
253 hydrodynamic wakes are also independent as the occurrence of one wake has no influence on any
254 other wake. Each wake is therefore an individual hydrodynamic patch. In Figures 3b and 3c,
255 despite the vegetation patches being closer together, there is still space in between them. Hence,
256 using the patch delineation guidelines proposed above, the vegetation can still be defined as a
257 cluster of distinct vegetation patches. However, this is not the case for the hydrodynamic wakes as
258 they now merge with each other and cannot be considered spatially separated. Figure 3b shows the
259 clearest form of interaction. Here the individual wakes are not indistinguishable at the
260 measurement scale and become one large wake, i.e. one large hydrodynamic patch. In Figure 3c,

261 the intermediate situation between Figures 3a and 3b is depicted. Here, the wakes are distinct
262 upstream, but subsequently merge to a certain extent downstream. We define this case, where the
263 vegetation patches are distinct, but their hydrodynamic influence zones are not, as a
264 “hydrodynamic patch-matrix” or “a matrix of hydrodynamic patches”. We must distinguish (e.g.
265 for the purposes of sampling or modelling) between the region of several individual hydrodynamic
266 patches (wakes) and the region of one merged hydrodynamic patch. Matrices of patches are made
267 up of distinct patches which nevertheless interact in some way. These distinctions can be seen as
268 analogous to those between ‘isolated roughness flow’ (c.f. Figure 3a), ‘skimming flow’ (c.f. Figure
269 3b) and ‘wake interference flow’ (Figure 3c), which were first proposed in the engineering
270 literature (Morris 1955) and which have been adopted in the ecohydrology literature more recently
271 (Davis & Barmuta 1989; Folkard 2011; Young 1992).

272
273 These different levels of interaction are illustrated by Sukhodolova (2008) and Sukhodolov and
274 Sukhodolova (2010), who studied the effect of different distributions of submerged vegetation (at
275 different times in the annual growth cycle in the same river reach) on turbulent flow structure in a
276 lowland river. Variation in the spatial properties of 233 vegetation patches over the growing season
277 changed the interaction between the hydrodynamic wakes. In the summer cases there was
278 relatively little separation between the patches, producing one combined hydrodynamic wake
279 patch (c.f. Figure 3b). In the early spring situations, when the vegetation was less developed,
280 individual vegetation patches producing individual hydrodynamic patches were observed (c.f.
281 Figure 3a). Finally, at intermediate vegetation patch separation, the individual vegetation patches
282 produced hydrodynamic patches which were at first distinct but subsequently merged, i.e. a
283 hydrodynamic patch matrix (c.f. Figure 3c). Another example of how systems can move from one
284 of these configurations to the others over time is provided by Vandenbruwaene et al. (2011), who

285 investigated the evolution of a tidal landscape undergoing colonisation by vegetation patches that
286 are laterally expanding in size and therefore grow closer to each other. Initially, the situation they
287 observed corresponded with Figure 3a, where the vegetation formed non-interacting patches (see
288 also Figure 1c). As the vegetation patches grew bigger and closer to each other, the high level of
289 influence between the hydrodynamic wakes made it impossible to define isolated hydrodynamic
290 patches, hence they moved first to the situation in Figure 3c, and ultimately to that in Figure 3b.

291
292 The often complex interactions between vegetation, fauna, hydrodynamics and sedimentary
293 processes that are studied in multidisciplinary studies imply that changes in any one of them can
294 alter the patch/patch-matrix structure in the others. Careful patch definition is particularly
295 important in measuring and modelling this kind of multi-faceted situation (Marion et al. 2014). An
296 example of this is provided in Figure 4.

297

298 4. Outlook

299 We now revisit the examples presented in Figure 1 and apply the 3 guidelines we have defined in
300 Section 3 to each of them. The Category I examples (Figures 1b and 1c) show patches whose
301 constitution is defined by vegetation shoot density, whose spatial properties are defined by sharp
302 edges, and which are individual patches in a shoot-density sense, but which may form inter-
303 connected matrices in terms of hydrodynamic, sedimentary conditions, macroinvertebrate
304 communities and/or substrate nutrient distributions. If these individual patches grow, they will
305 move from patches that are isolated in every sense (c.f. Figure 3a) to interacting matrices of
306 individual patches (c.f. Figure 3c, then Figure 3b) to single, merged patches. Thus, while the
307 delineation of the vegetation patches, for example for the purposes of measuring their size and
308 shape, is relatively unambiguous, their sampling for macroinvertebrate, sediment or hydrodynamic

309 parameters requires careful consideration of the extent to which they form a matrix in these terms.
310 Moreover, understanding the role they play in affecting hydrodynamic, sedimentary or
311 macroinvertebrate conditions requires an appreciation of their matrix-scale interactions.

312

313 The Category II examples (Figures 1e and 1f) show patches defined again by vegetation shoot
314 density. How to delineate them is less clear than for Category I cases, but the guideline defined in
315 Section 3b provides an unambiguous way of achieving this. Interactions between patches in
316 situations such as these are likely to be enhanced by the presence of regions of lower vegetation
317 density between defined patches, and thus matrix-scale structures are likely to be more important
318 here than in Category I cases.

319

320 The Category III case shown in Figure 1h contains what may be considered to be a single
321 vegetation patch, or a series of separate patches of different vegetation species, depending on how
322 the constitution of the patches is defined. Macroinvertebrate, sedimentary and hydrodynamic
323 parameter patch configuration in these conditions may be similar or different between the patches
324 of different species depending on the similarity or difference of the plants' morphologies and their
325 interactions with these parameters. As with Category II, although the spatial properties of each
326 patch may appear difficult to define at first sight, the guidelines we provide give a clear way of
327 identifying the edge of each patch, depending on the parameter that defines it.

328

329 Finally, the Category IV example shown in Figure 1j can be clearly described in terms of the
330 guidelines for investigating patch interactions (Section 3c) as two vegetation patches and one
331 hydrodynamic patch matrix (with flow direction, visualised by the tracers shown, as the

332 hydrodynamic parameter under consideration). These are also likely to have merged, matrix-scale
333 configurations of sediment and macroinvertebrate communities.

334

335 Thus, our guidelines of patch and matrix-scales provide a comparative framework within which
336 understanding of these disparate contexts can be brought together. They also imply the need for
337 further numerical and laboratory modelling efforts. Investigations are required of the matrix-scale
338 connectivity of patches in terms of the wide variety of variables considered above. Studies of the
339 effects of gradual changes in parameters such as shoot density, rather than the sharp-edged patch
340 configurations that have heretofore been used in physical and numerical modelling studies are
341 required. Studies of mixed patches (for example, patches made up of more than one
342 species/morphology of vegetation) are also virtually non-existent in the literature and require
343 attention. In some cases, absolute-value thresholds might be appropriate (e.g. a fixed altitude to
344 delineate bathymetry), while boundaries defined by gradient-maxima, absolute gradient values or
345 other measures might be more appropriate in other situations. This variety of threshold definitions
346 can be easily accommodated within GIS-software packages. Once patches are defined, other
347 software can be used to analyse them (e.g. Fragstats).

348

349 In conclusion: we provided a relatively rigid method to approach the identification and delineation
350 of patches and patch-matrices, which also serves as a platform for consistency across studies. We
351 have provided a framework that can give consistent guidance in situations where patch definition
352 may be ambiguous. Our intention is that, as well as providing a framework within which studies
353 from different environmental contexts can be meaningfully compared and mutually enhanced, the
354 definitions and guidelines proposed here also provide a means for strengthening the mutual support

355 of field, physical and numerical modelling studies of complex interacting systems such as those
356 considered in this paper.

357

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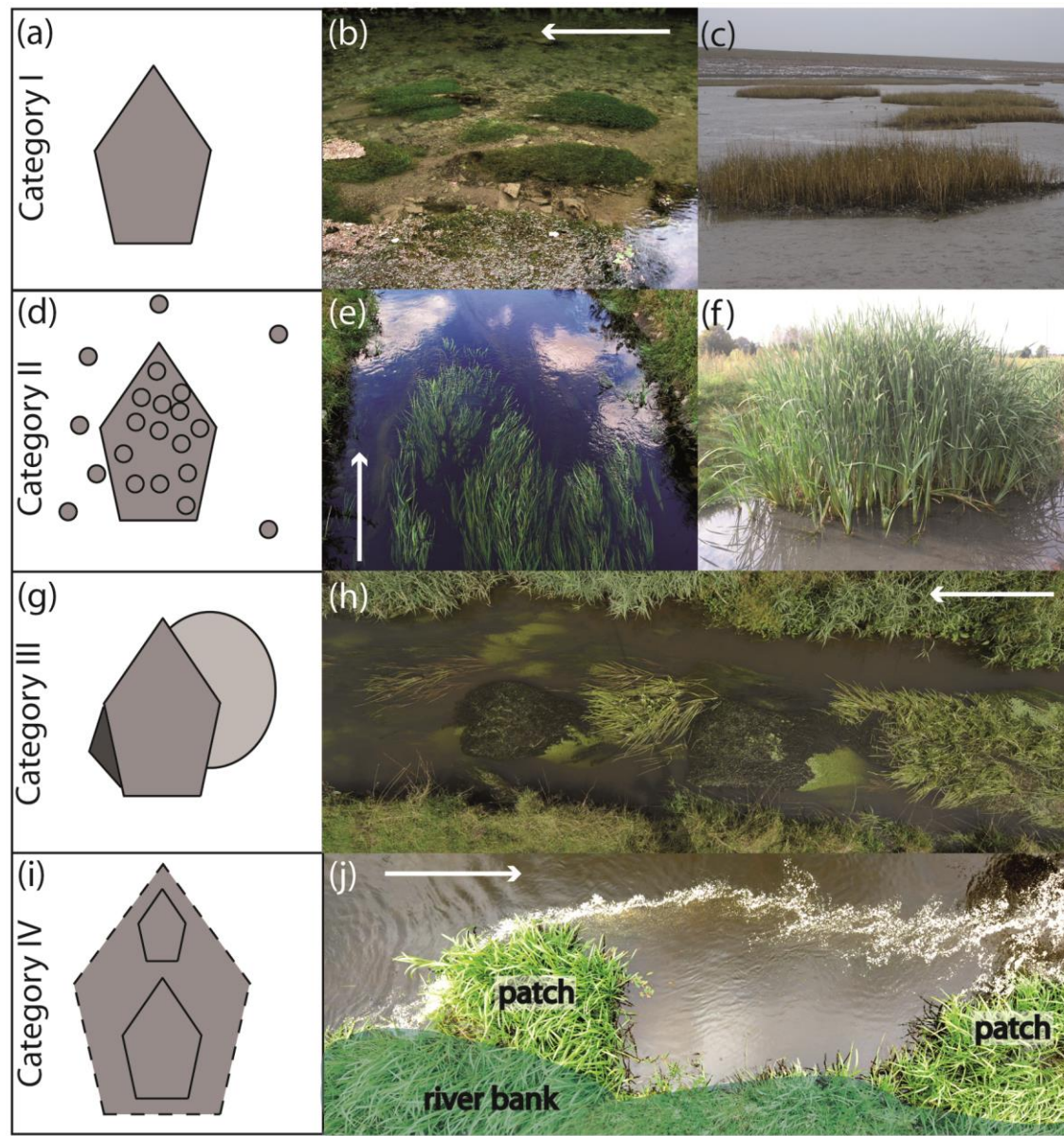
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361 **References**

- 362 Bal K, Brion N, Woulé-Ebongué V, Schoelynck J, Jooste A, Barrón C, Dehairs F, Meire P, Bouma
363 T (2013) Influence of hydraulics on the uptake of ammonium in two freshwater aquatic plants.
364 *Freshw. Biol.* 58(12): 2452-2463
- 365 Bouma TJ, Friedrichs M, van Wesenbeeck BK, Temmerman S, Graf G, Herman PMJ (2009)
366 Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal
367 macrophyte *Spartina anglica*. *Oikos* 118(2): 260-268
- 368 Bouma TJ, Temmerman S, van Duren LA, Martini E, Vandenbruwaene W, Callaghan DP, Balke
369 T, Bierman G, Klaassen PC, van Steeg P, Dekker F, van de Koppel J, de Vries MB, Herman PMJ
370 (2013) Organism traits determine the strength of scale-dependent bio-geomorphic
371 feedbacks: A flume study on three intertidal plant species. *Geomorphology* 180-181: 57-65
- 372 Bouma TJ, van Duren LA, Temmerman S, Claverie T, Blanco-Garcia A, Ysebaert T, Herman PMJ
373 (2007) Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining
374 field, flume and modelling experiments. *Cont. Shelf Res.* 27(8): 1020-1045
- 375 Creëlle S, Roldan R, Herremans A, Meire D, Buis K, Meire P, Van Oyen T, De Mulder T, Troch P
376 (in press) Validation of large-scale particle image velocimetry to acquire free-surface flow fields
377 in vegetated rivers. *Journal of applied water engineering and research*: doi:
378 10.1080/23249676.23242016.21251856
- 379 Davis JA, Barmuta LA (1989) An ecologically useful classification of mean and near-bed flows in
380 streams and rivers. *Freshw. Biol.* 21(2): 271-282
- 381 Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends Ecol. Evol.* 17(4): 177-183
- 382 Folkard AM (2011) Flow regimes in gaps within stands of flexible vegetation: laboratory flume
383 simulations. *Environmental Fluid Mechanics* 11(3): 289-306
- 384 Francis RA, Corenblit D, Edwards PJ (2009) Perspectives on biogeomorphology, ecosystem
385 engineering and self-organisation in island-braided fluvial ecosystems. *Aquat. Sci.* 71(3): 290-304
- 386 Gibbins C, Vericat D, Batalla RJ (2007) When is stream invertebrate drift catastrophic? The role
387 of hydraulics and sediment transport in initiating drift during flood events. *Freshw. Biol.* 52(12):
388 2369-2384
- 389 Gurnell AM (2014) Plants as river system engineers. *Earth Surf. Process. Landf.* 39(1): 4-25
- 390 Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New*
391 *Phytol.* 162(1): 9-24
- 392 Hutchings MJ, Wijesinghe DK (2008) Performance of a clonal species in patchy environments:
393 effects of environmental context on yield at local and whole-plant scales. *Evolutionary Ecology*
394 22(3): 313-324
- 395 Kleeberg A, Kohler J, Sukhodolova T, Sukhodolov A (2010) Effects of aquatic macrophytes on
396 organic matter deposition, resuspension and phosphorus entrainment in a lowland river. *Freshw.*
397 *Biol.* 55(2): 326-345
- 398 Lancaster J, Hildrew AG (1993) Characterizing in-stream flow refugia. *Can. J. Fish. Aquat. Sci.*
399 50(8): 1663-1675
- 400 Li H, Reynolds JF (1995) On definition and quantification of heterogeneity. *Oikos* 73(2): 280-284
- 401 Maldonado M, Riesgo A, Bucci A, Rutzler K (2010) Revisiting silicon budgets at a tropical
402 continental shelf: Silica standing stocks in sponges surpass those in diatoms. *Limnol. Oceanogr.*
403 55(5): 2001-2010
- 404 Marion A, Nikora V, Puijalon S, Bouma T, Koll K, Ballio F, Tait S, Zaramella M, Sukhodolov A,
405 O'Hare M, Wharton G, Aberle J, Tregnaghi M, Davies P, Nepf H, Parker G, Statzner B (2014)
406 Aquatic interfaces: a hydrodynamic and ecological perspective. *Journal of Hydraulic Research*
407 52(9): 744-758
- 408 Morris EP, Peralta G, Brun FG, van Duren L, Bouma TJ, Perez-Llorens JL (2008) Interaction
409 between hydrodynamics and seagrass canopy structure: Spatially explicit effects on ammonium
410 uptake rates. *Limnol. Oceanogr.* 53(4): 1531-1539

- 411 Morris HM (1955) A new concept of flow in rough conduits. *Trans Am Soc Civ Eng* 120: 373–398
- 412 Mulderij G, Mau B, Domis LND, Smolders AJP, Van Donk E (2009) Interaction between the
413 macrophyte *Stratiotes aloides* and filamentous algae: does it indicate allelopathy? *Aquat. Ecol.*
414 43(2): 305-312
- 415 Naden P, Rameshwaran P, Mountford O, Robertson C (2006) The influence of macrophyte
416 growth, typical of eutrophic conditions, on river flow velocities and turbulence production. *Hydrol.*
417 *Process.* 20(18): 3915-3938
- 418 O'Hare MT (2015) Aquatic vegetation - a primer for hydrodynamic specialists. *Journal of Hydraulic*
419 *Research* 53(6): 687-698
- 420 Opdekamp W, Teuchies J, Vrebos D, Chormanski J, Schoelynck J, Van Diggelen R, P. M, E. S
421 (2012) Tussocks: biogenic silica hot-spot in a riparian wetland. *Wetlands* 32(6): 1115-1124
- 422 Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and
423 catastrophic shifts in ecosystems. *Science* 305(5692): 1926-1929
- 424 Rietkerk M, Van de Koppel J (2008) Regular pattern formation in real ecosystems. *Trends Ecol.*
425 *Evol.* 23(3): 169-175
- 426 Sand-Jensen K (1998) Influence of submerged macrophytes on sediment composition and near-
427 bed flow in lowland streams. *Freshw. Biol.* 39(4): 663-679
- 428 Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH,
429 Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. *Nature* 461(7260): 53-
430 59
- 431 Schoelynck J, Bal K, Verschoren V, Penning E, Struyf E, Bouma T, Meire D, Meire P, Temmerman
432 S (2014) Different morphology of *Nuphar lutea* in two contrasting aquatic environments and its
433 effect on ecosystem engineering. *Earth Surf. Process. Landf.* 39: 2100-2108
- 434 Schoelynck J, De Groote T, Bal K, Vandenbruwaene W, Meire P, Temmerman S (2012) Self-
435 organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation.
436 *Ecography* 35(8): 760-768
- 437 Sukhodolov AN, Sukhodolova TA (2010) Case Study: Effect of Submerged Aquatic Plants on
438 Turbulence Structure in a Lowland River. *Journal of Hydraulic Engineering-Asce* 136(7): 434-446
- 439 Sukhodolova T (2008) Studies of turbulent flow in vegetated river reaches with implications for
440 transport and mixing processes. In: *Mathematisch-Naturwissenschaftliche Fakultät II. Humboldt-*
441 *Universität zu Berlin.*
- 442 Thums M, Bradshaw CJA, Sumner MD, Horsburgh JM, Hindell MA (2013) Depletion of deep
443 marine food patches forces divers to give up early. *Journal of Animal Ecology* 82(1): 72-83
- 444 Townsend CR (1989) The Patch Dynamics Concept of Stream Community Ecology. *Journal of*
445 *the North American Benthological Society* 8(1): 36-50
- 446 Turner SR, Taylor N, Jones L (2001) Mutations of the secondary cell wall. *Plant Molecular Biology*
447 47(1-2): 209-219
- 448 van de Koppel J, Crain CM (2006) Scale-dependent inhibition drives regular tussock spacing in a
449 freshwater marsh. *Am. Nat.* 168(5): E136-E147
- 450 van Wesenbeeck BK, van de Koppel J, Herman PMJ, Bouma TJ (2008) Does scale-dependent
451 feedback explain spatial complexity in salt-marsh ecosystems? *Oikos* 117(1): 152-159
- 452 Vandenbruwaene W, Temmerman S, Bouma TJ, Klaassen PC, de Vries MB, Callaghan DP, van
453 Steeg P, Dekker F, van Duren LA, Martini E, Balke T, Biermans G, Schoelynck J, Meire P (2011)
454 Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a
455 tidal landscape. *Journal of Geophysical Research* 116(F1): F01008
- 456 Verschoren V, Schoelynck J, Buis K, Visser F, Meire P, Temmerman S (2017) Mapping the spatio-
457 temporal distribution of key vegetation cover properties in lowland river reaches, using digital
458 photography. *Environ. Monit. Assess.* 189(6): 294
- 459 Visser F, Buis K, Verschoren V, Meire P (2015) Depth Estimation of Submerged Aquatic
460 Vegetation in Clear Water Streams Using Low-Altitude Optical Remote Sensing. *Sensors* 15:
461 25287-25312

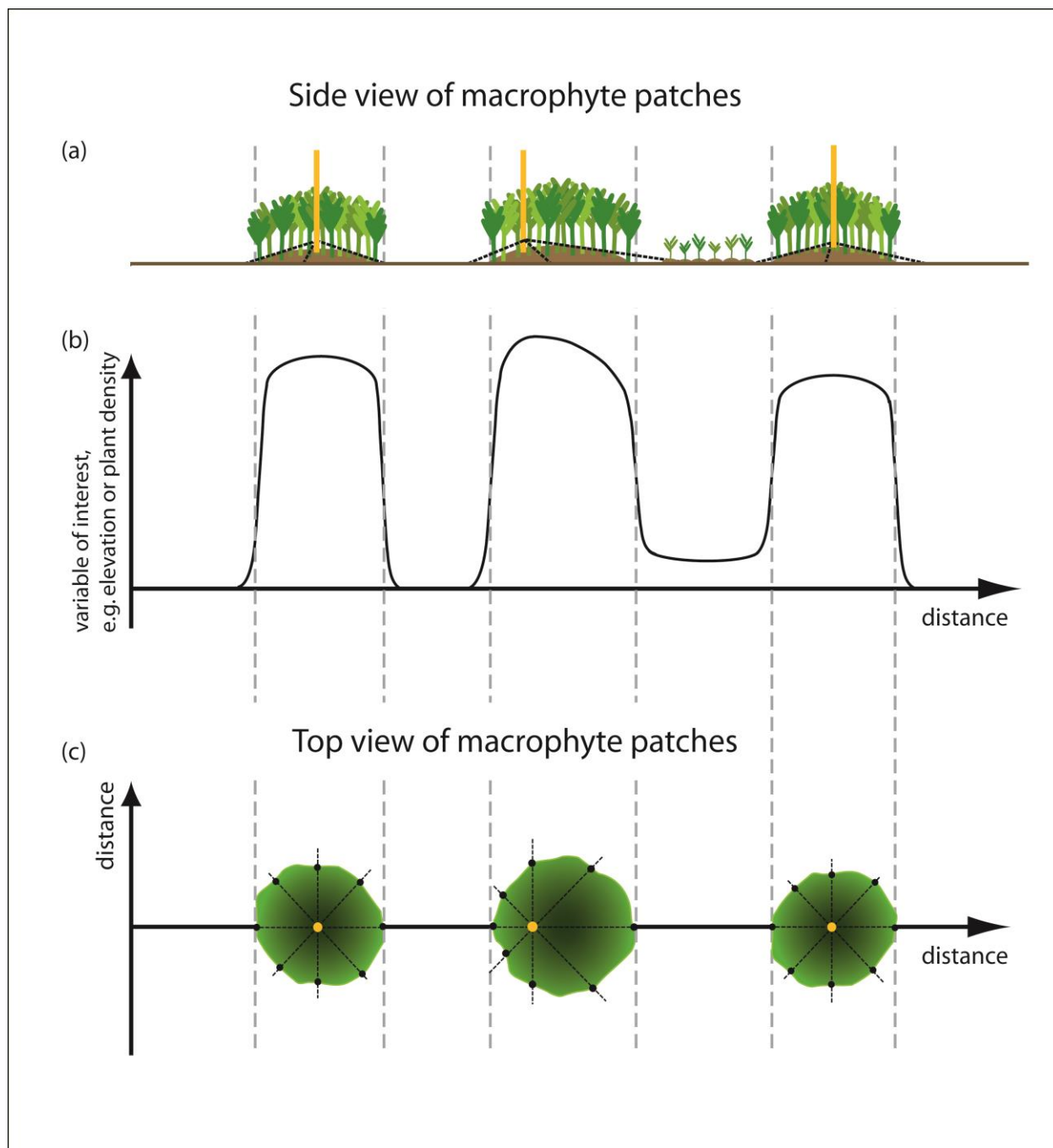
- 462 Wagner HH, Fortin MJ (2005) Spatial analysis of landscapes: Concepts and statistics. *Ecology*
463 86(8): 1975-1987
- 464 Weerman EJ, Van Belzen J, Rietkerk M, Temmerman S, Kefi S, Herman PMJ, Van de Koppel J
465 (2012) Changes in diatom patch-size distribution and degradation in a spatially self-organized
466 intertidal mudflat ecosystem. *Ecology* 93(3): 608-618
- 467 Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species
468 richness at the landscape scale. *Oecologia* 132(1): 96-101
- 469 Young WJ (1992) Clarification of the criteria used to identify near-bed flow regimes. *Freshw. Biol.*
470 28(3): 383-391
- 471
- 472

473 **Figures**

474

475 **Figure 1.** Examples of different vegetation patch categories. White arrows indicate mean flow
 476 direction. (a) Category I, well-delineated, single species patches, e.g. (b) *Ranunculus sp.* in a river;
 477 (c) Cord-grass [*Spartina anglica*] on tidal mudflats. (d) Category II, single species patches, poorly
 478 delineated (circles represent single shoots), e.g. (e) Bur-reed [*Sparganium emersum*] in a river; (f)
 479 Bulrush [*Typha latifolia*] by a lake. (g) Category III, multiple species growing together, e.g. (h) at
 480 least five different submerged species in a river. (i) Category IV, delineated vegetation patches

- 481 acting hydrodynamically as one, e.g. (j) two reed canary grass patches [*Phalaris arundinacea*]
482 with a combined effect on the flow (visualised by white tracers).

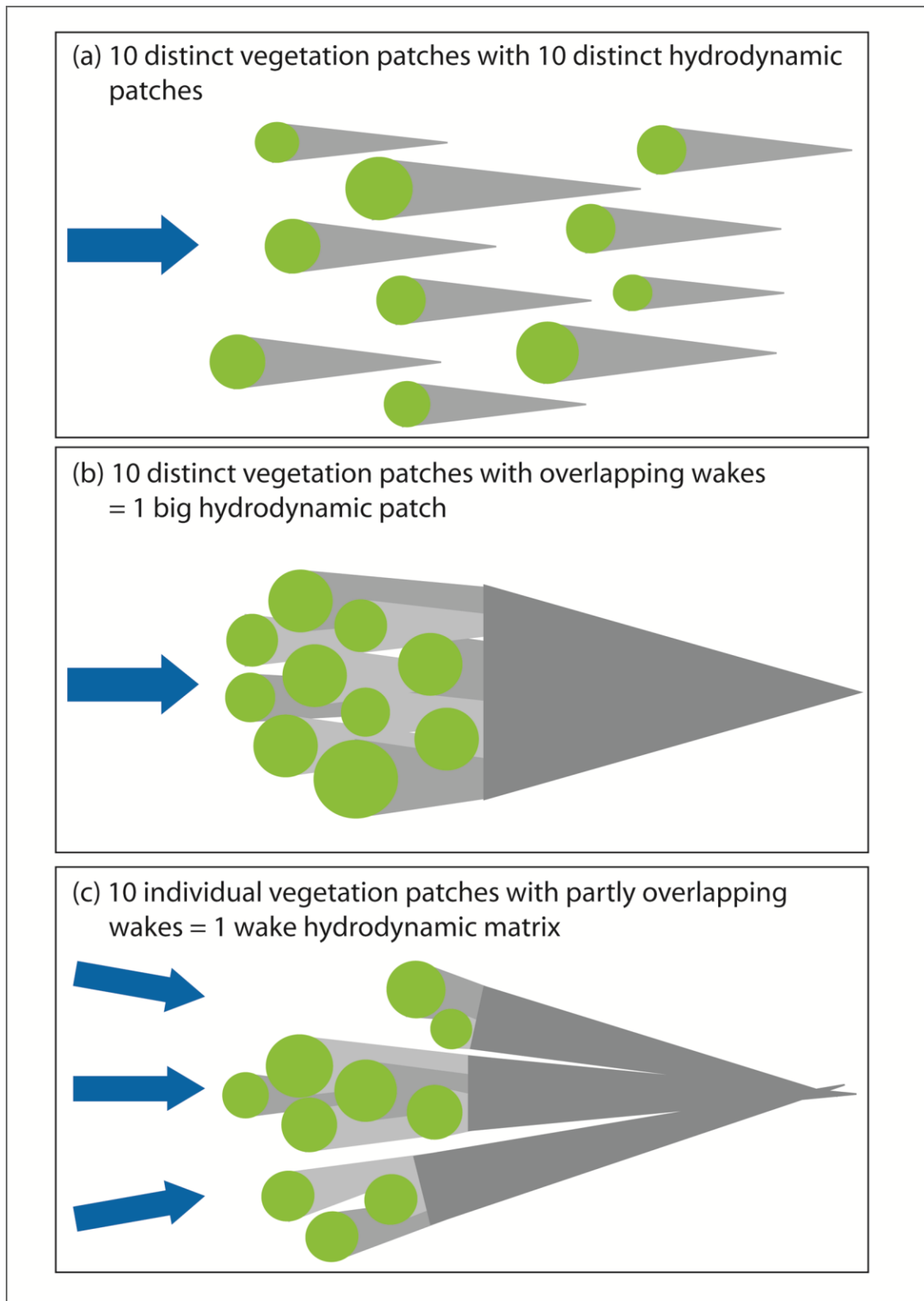


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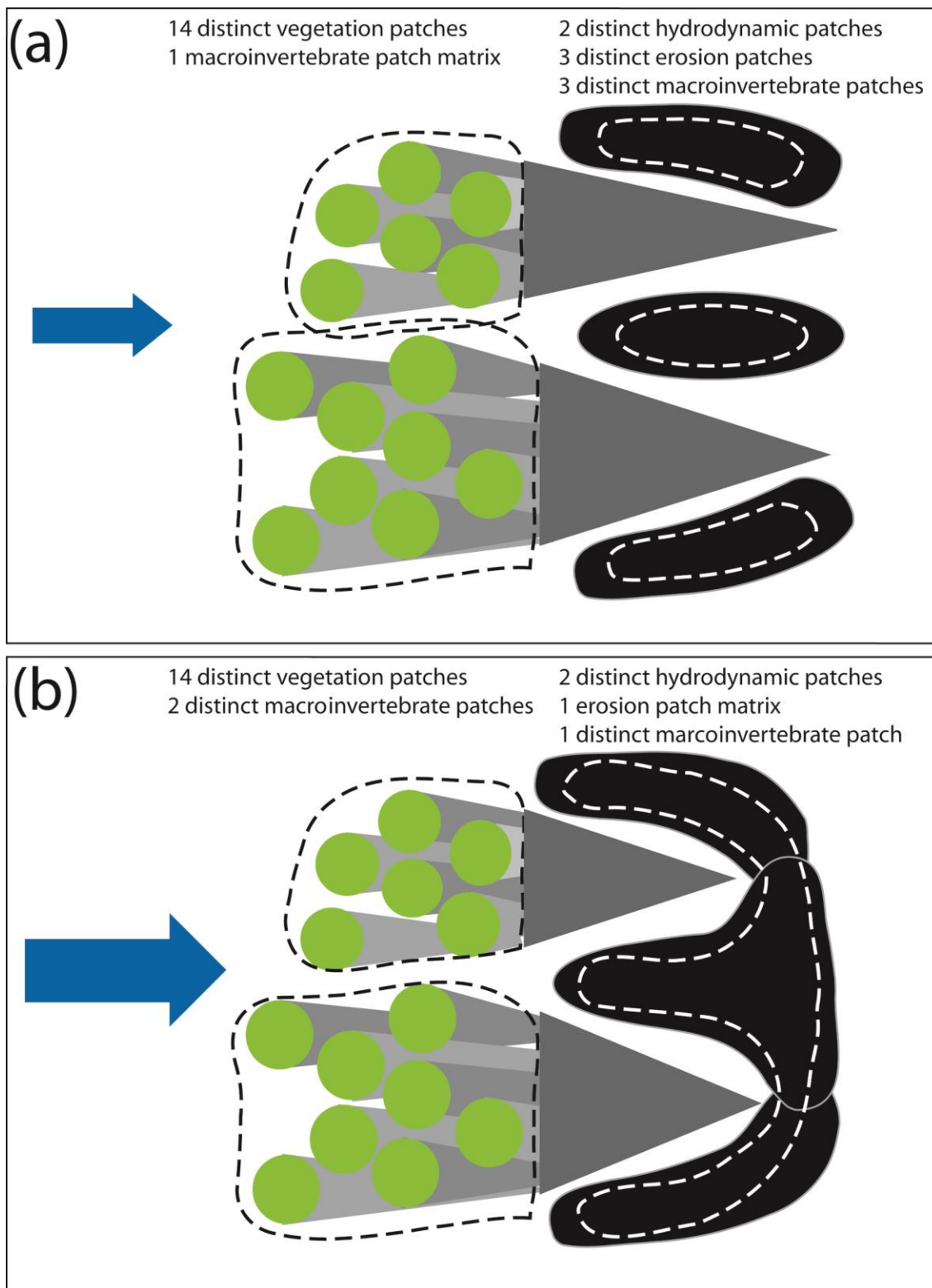
484 **Figure 2.** Definition diagram for patch edge identification method. Panel (a) shows the side view
 485 of the spatial distribution of vegetation. The vegetation on the left side is quite straightforward to
 486 identify as a patch, but the cluster of vegetation on the right side is somewhat ambiguous. To
 487 determine the patch edges, we choose the local maximum within each patch (yellow line in panel
 488 a, yellow dot in panel c), and draw radial lines in all directions (black dashed lines, panel c). The

489 points where the change of the variable of interest (panel b) is at its maximum (vertical grey dashed
490 lines) are joined up to create the patch boundary (panel c). As a result, we have now identified and
491 delineated three distinct patches following the same guidelines.

492



494 **Figure 3.** Guideline diagram to distinguish individual patches from patch matrices. Blue arrows
495 indicate the angle of attack of the incoming flow. Panel (a) shows 10 distinct vegetation patches
496 (green circles) and 10 distinct hydrodynamic patches (grey triangles). Panel (b) shows 10
497 individual vegetation patches and 1 hydrodynamic patch (dark grey triangle). Panel (c) shows 10
498 distinct vegetation patches and 1 hydrodynamic patch matrix because the different hydrodynamic
499 wake zones interact.



500

501 **Figure 4.** (a) Plan view sketch illustrating interactions between vegetation, hydrodynamic,

502 macroinvertebrate and erosion patches. Blue arrows show flow direction; green circles indicate

503 macrophyte patches; grey triangles indicate hydrodynamic patches (wakes) according to figure 3b;
504 black areas indicate erosion patches (scour zones); black dashed lines indicate patches of low-flow
505 favouring limnophilic macroinvertebrates such as *Asselus aquaticus*; white dashed lines indicate
506 patches of high-flow favouring rheophilic macroinvertebrates such as *Rhitrogena germanica*. (b)
507 Higher flow has a negative effect on the connectivity of the low-flow macroinvertebrates, but may
508 cause stronger merging of the erosion patches with a positive effect on the connectivity of high-
509 flow macroinvertebrates.