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

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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 <u>1. Why do we need these guidelines?</u>

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

2. Examples of macrophyte patches in aquatic environments

In some cases, macrophyte patches are easily and rather unambiguously defined, whereas in many other situations, especially in aquatic habitats, the delineation of patches is less straightforward (Kolasa 2014). For example: plant patches identified in aquatic environments can be categorised into four groups. In the first category, plant patches are easily recognised (Figure 1a). These consist of a single species at a relatively high density within patches whose edges are sharp. This category appears especially in subaqueous systems (Figure 1b). It is also frequently found on mudflats where patches of pioneer plants are formed by the establishment of a few individual plants that then expand clonally (Figure 1c). In the second category (Figure 1d), patches still consist of a single species, but the edges are less sharp because the density of shoots does not change quasi-discontinuously as in the first category; instead the patch fades into areas better identified as collections of isolated individual shoots. This configuration is often found in subaqueous systems where a group of individuals emerges from a seed bank (Figure 1e), and can also occur at the edges of lakes or marshes (Figure 1f). In the third category (Figure 1g), patches consist of two or more species. This is common in subaqueous systems where single shoots of different species grow in amongst each other, or where stands of different species are interwoven (Figure 1h). Finally, in the fourth category (Figure 1i), two or more patches of the same or of different species grow separately, but interact with each other in such a way that they can be regarded as one under certain circumstances (see later). This category is frequently found in the field (e.g. Figure 1j), and includes situations where it is difficult to demarcate the outer edges of the region of the patches' mutual interaction with the flow of water, and hence its size. From these four categories, we 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   <u>3. Guidelines for defining a patch</u>

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. O*ur 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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360

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473 **Figures**
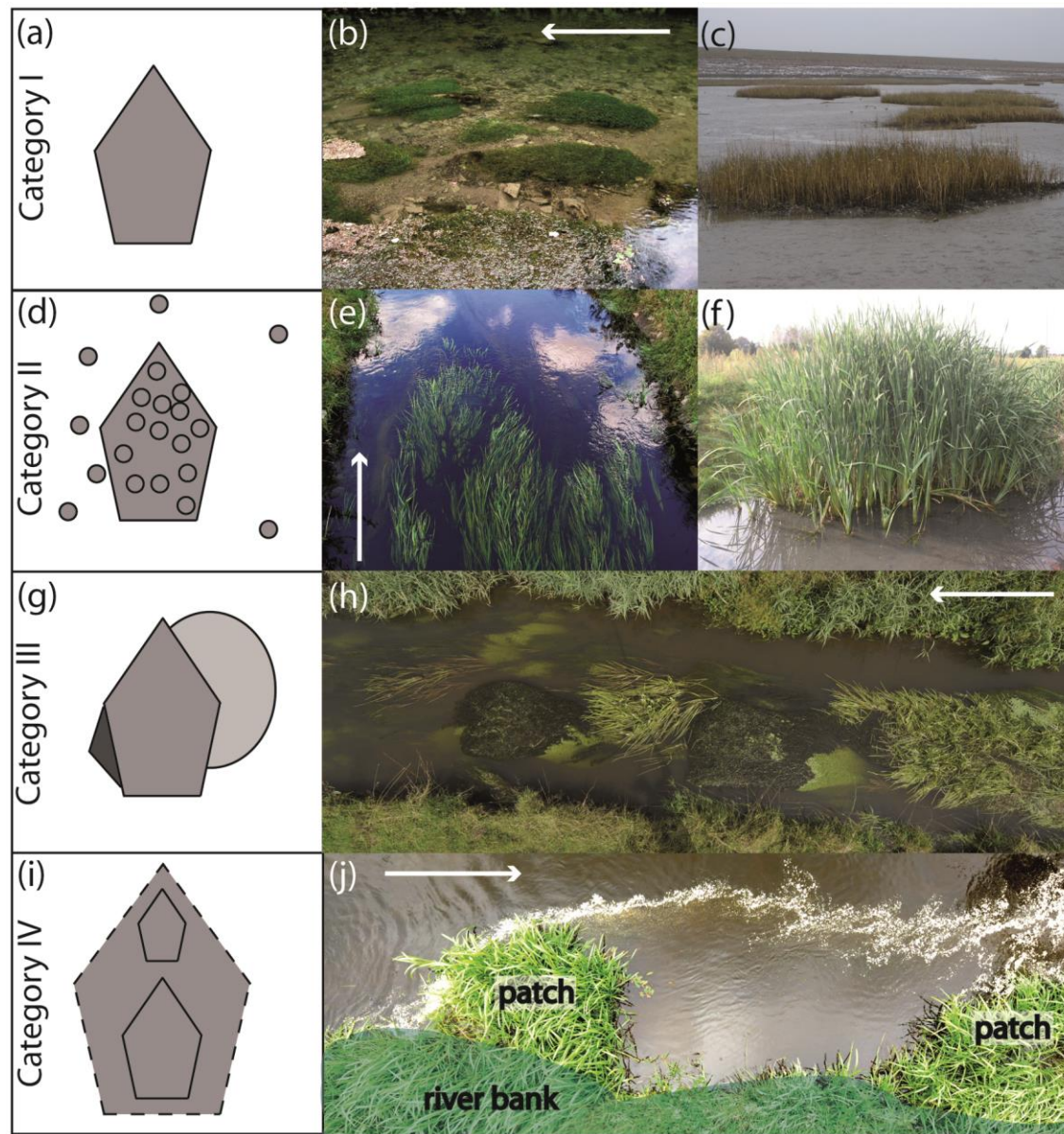
474

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).
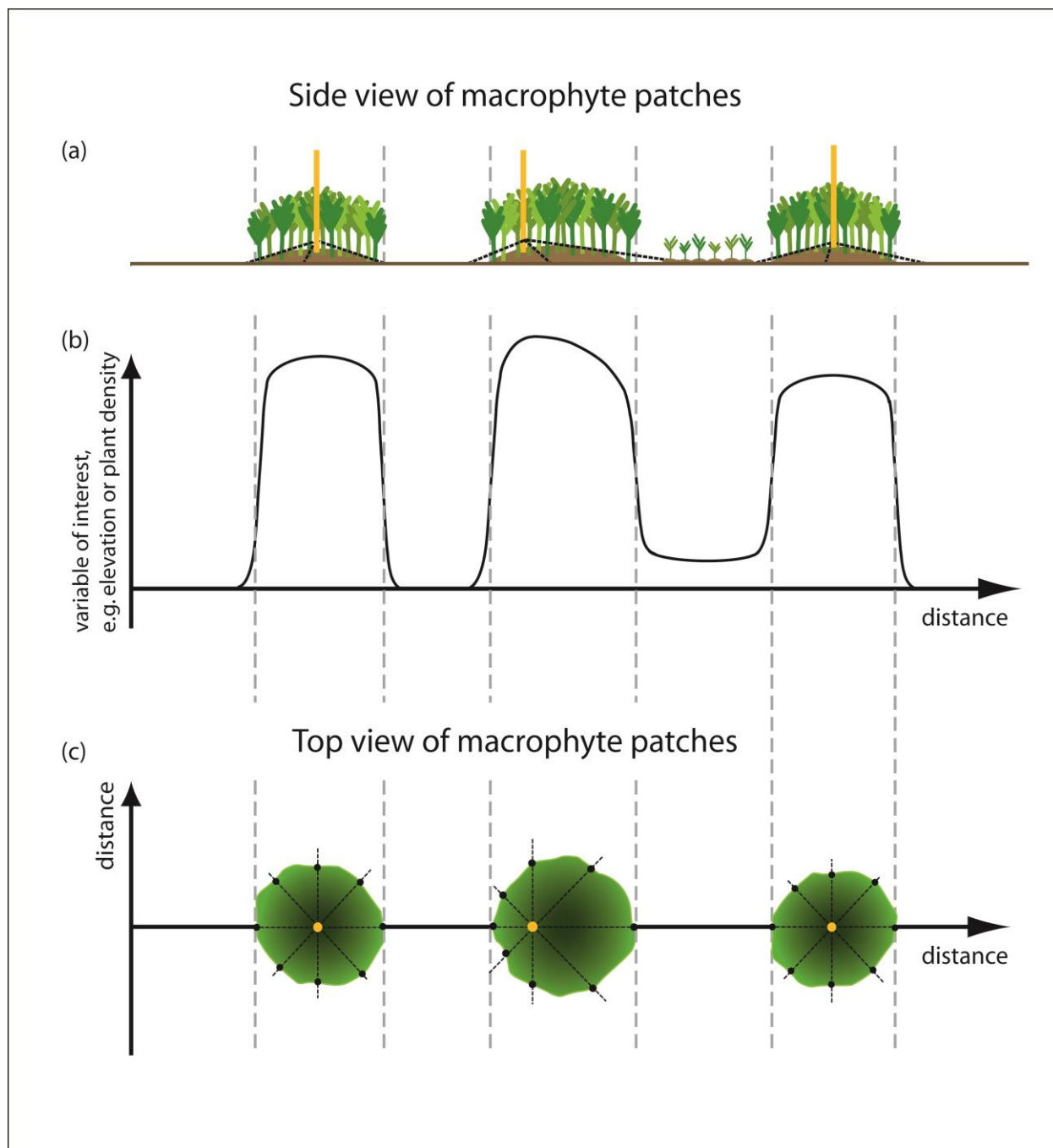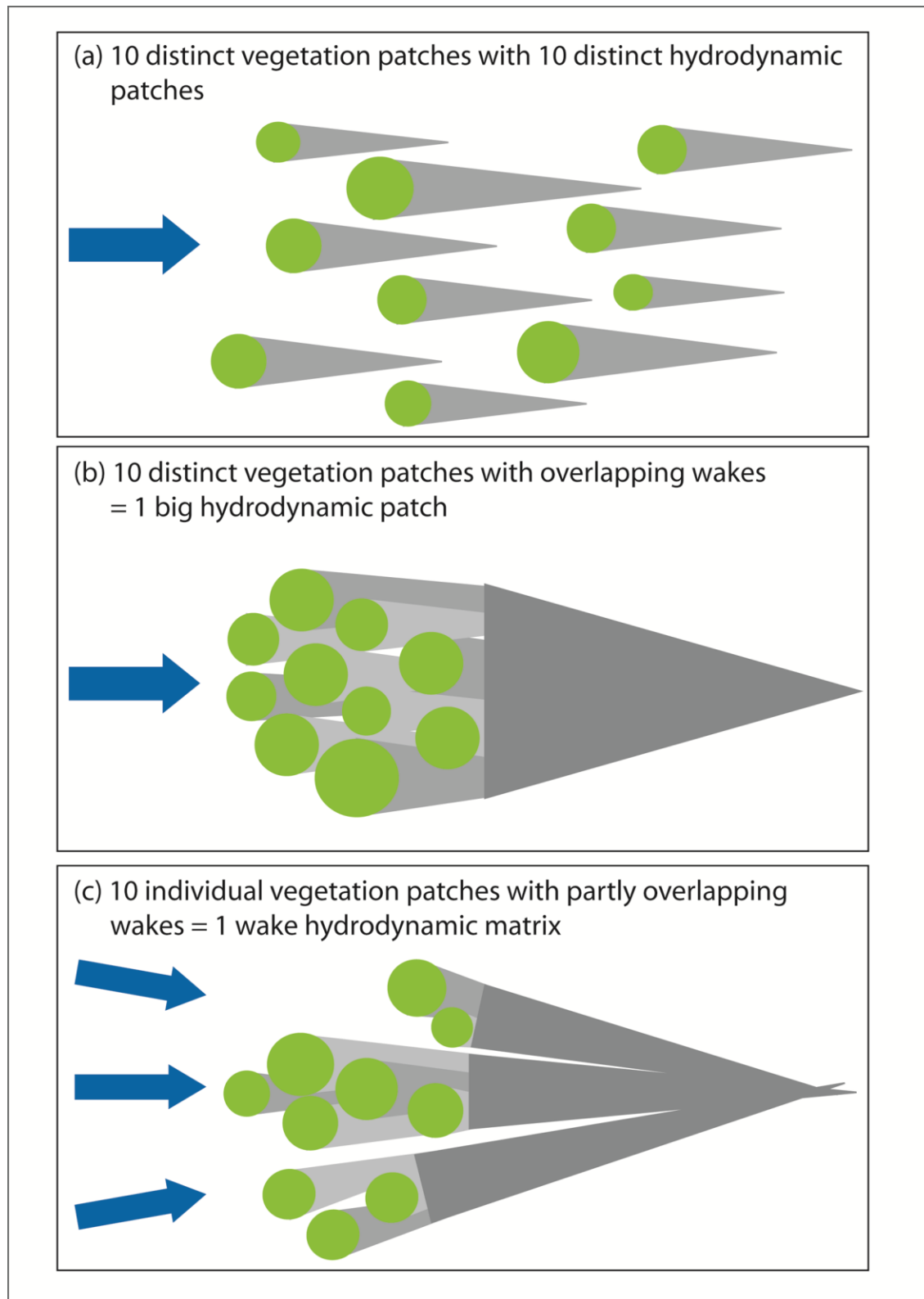
Figure 2. Definition diagram for patch edge identification method. Panel (a) shows the side view of the spatial distribution of vegetation. The vegetation on the left side is quite straightforward to identify as a patch, but the cluster of vegetation on the right side is somewhat ambiguous. To determine the patch edges, we choose the local maximum within each patch (yellow line in panel 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

(a) 10 distinct vegetation patches with 10 distinct hydrodynamic patches

(b) 10 distinct vegetation patches with overlapping wakes = 1 big hydrodynamic patch

(c) 10 individual vegetation patches with partly overlapping wakes = 1 wake hydrodynamic matrix

493

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.
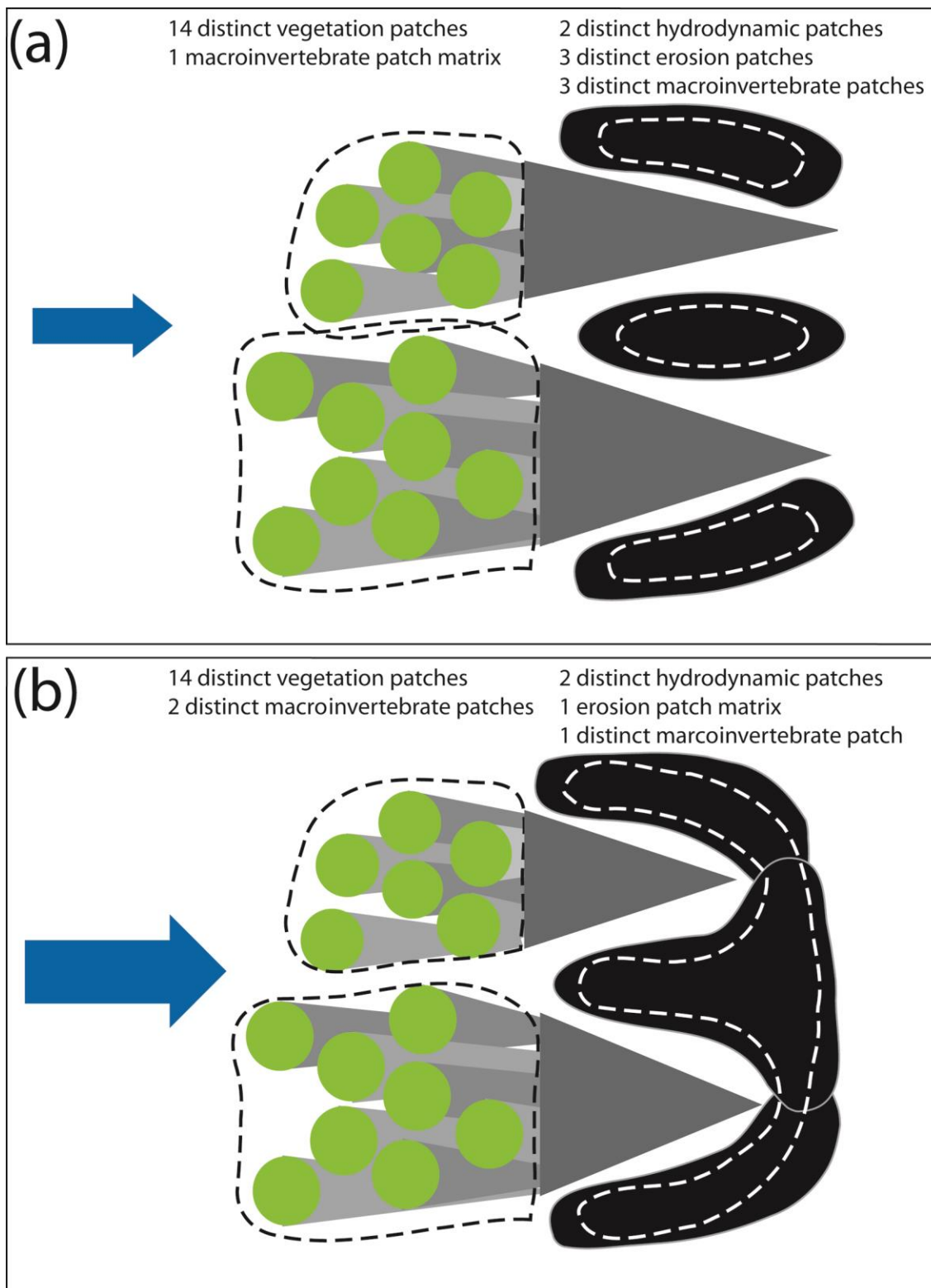
Figure 4. (a) Plan view sketch illustrating interactions between vegetation, hydrodynamic, macroinvertebrate and erosion patches. Blue arrows show flow direction; green circles indicate

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.