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

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Abstract

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

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

**Main Text**

1. Why do we need these guidelines?

Self-organised patch formation is a process whereby large-scale ordered spatial patterns emerge from disordered initial conditions through local interactions between organisms and their environment (Rietkerk & Van de Koppel 2008). This process has recently gained increased scientific attention because it has important implications for ecosystem functioning. Patchiness may be interpreted as an early warning sign of tipping points in ecosystems at which a sudden shift to a contrasting regime may occur (Scheffer et al. 2009). Self-organised patch formation can also increase ecosystem productivity as well as resilience and resistance to global environmental change, compared to spatially homogeneous ecosystems (Rietkerk & Van de Koppel 2008).

Patches are also important in facilitating the colonization of initially bare landscapes and their subsequent bio-geomorphic evolution (Gurnell 2014; Vandenbruwaene et al. 2011), and they also have a role in regulating fluxes of water (Rietkerk et al. 2004) and sediments (van Wesenbeeck et al. 2008). Correct delineation of patches is therefore extremely important (Li & Reynolds 1995), especially in multidisciplinary studies where every specialist may define patches differently (O’Hare 2015).
The term “patch” is commonly used in aquatic ecology to distinguish, for instance: (i) patches of vegetation from surrounding bare areas, e.g. within rivers and lakes (Kleeberg et al. 2010; Naden et al. 2006; Schoelynck et al. 2014; Schoelynck et al. 2012), on river floodplains (Francis et al. 2009; Gurnell 2014), in riparian wetlands (Opdekamp et al. 2012), or on intertidal floodplains (Bouma et al. 2009; Bouma et al. 2013; Bouma et al. 2007; Vandenbruwaene et al. 2011), (ii) diatom aggregations from bare tidal mudflats (Weerman et al. 2012); (iii) zones with fine sediment from zones with coarser grain sizes (Gibbins et al. 2007); (iv) nutrient-rich from nutrient-poor zones (Hodge 2004; Hutchings & Wijesinghe 2008); (v) zones of high hydrodynamic stress from more quiescent zones (Lancaster & Hildrew 1993); (vi) coral reefs from sea grass beds (Maldonado et al. 2010); (vii) food-rich from food-depleted locations (Thums et al. 2013), (viii) zones of high variability in populations of soil organisms from zones with less variability (Ettema & Wardle 2002) and even (ix) areas modified by ecosystem engineers (Wright et al. 2002), from areas not modified in this way. The implication common to all of these examples (and the many others in which the term is used (Townsend 1989)) is that patches are areas characterised by values of a parameter of interest that are relatively high or low compared to the mean value across the whole area being studied. As such, patches tend to be viewed in two ways. Firstly, in synoptic scale studies, they are identified as the lower limit of structural detail, for example where a landscape is characterised in terms of the size and shape statistics of patches of a certain kind of habitat (e.g. Visser et al. (2015), who used low-altitude imaging to map submerged aquatic vegetation patches). Secondly, in studies executed via point measurements, they are identified as the upper limit of contextual structure, for example where comparisons are made between measurements within and outside of patches. Thus, a patch has a finite spatial extent (distinguishing it from a “point”) but is smaller than the entire study area.
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
constitution – i.e. the variable(s) whose values define the patch; (b) their extent – i.e. identification of patch boundaries; and (c) their distinction – i.e. distinguishing multiple separate-but-interacting patches from single patches.

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

3. Guidelines for defining a patch

Guideline 1: define the constitution of the patch

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

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

Guideline 2: define the spatial properties of the patch

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

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

To address this issue, we now provide a practical guideline for defining and delineating patches. We first identify relevant scales that contextualise our definition. At the upper end, the “domain” scale is the scale of the entire region of interest – for example, the experimental section of a
laboratory facility or mesocosm, the entire domain of a numerical model, or the field site in which we are working. At the lower end, the “individual element” scale is the smallest scale of objects we are focusing on - for example, single shoots if we are studying vegetation, or single sediment particles if we are studying bed material. The “measurement” scale depends on the mode of measurement and consists of a resolution and a footprint. The resolution is the density of measurement points within the domain (e.g. the number of sediment cores per transect). The footprint is the area covered by the measurement point (e.g. the cross-sectional area of the corer). We assume that the measurement scale (both resolution and footprint) is coarser than the individual element scale, thus enabling meaningful measurement of the density of individual elements. If this is not the case, we would not define the observed distribution to be patchy, but as being made up of isolated individual elements.

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

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

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

Guideline 3: define the distinction or interaction between patches

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

In Figure 3a, the areas of vegetation are well-separated from each other. Thus, it is appropriate to consider each of these areas as an individual patch of vegetation. In this scenario, all of the hydrodynamic wakes are also independent as the occurrence of one wake has no influence on any other wake. Each wake is therefore an individual hydrodynamic patch. In Figures 3b and 3c, despite the vegetation patches being closer together, there is still space in between them. Hence, using the patch delineation guidelines proposed above, the vegetation can still be defined as a cluster of distinct vegetation patches. However, this is not the case for the hydrodynamic wakes as they now merge with each other and cannot be considered spatially separated. Figure 3b shows the clearest form of interaction. Here the individual wakes are not indistinguishable at the measurement scale and become one large wake, i.e. one large hydrodynamic patch. In Figure 3c,
the intermediate situation between Figures 3a and 3b is depicted. Here, the wakes are distinct upstream, but subsequently merge to a certain extent downstream. We define this case, where the vegetation patches are distinct, but their hydrodynamic influence zones are not, as a “hydrodynamic patch-matrix” or “a matrix of hydrodynamic patches”. We must distinguish (e.g. for the purposes of sampling or modelling) between the region of several individual hydrodynamic patches (wakes) and the region of one merged hydrodynamic patch. Matrices of patches are made up of distinct patches which nevertheless interact in some way. These distinctions can be seen as analogous to those between ‘isolated roughness flow’ (c.f. Figure 3a), ‘skimming flow’ (c.f. Figure 3b) and ‘wake interference flow’ (Figure 3c), which were first proposed in the engineering literature (Morris 1955) and which have been adopted in the ecohydrology literature more recently (Davis & Barmuta 1989; Folkard 2011; Young 1992).

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

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

4. Outlook

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

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

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

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

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

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

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References


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

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
points where the change of the variable of interest (panel b) is at its maximum (vertical grey dashed lines) are joined up to create the patch boundary (panel c). As a result, we have now identified and delineated three distinct patches following the same guidelines.
(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
Figure 3. Guideline diagram to distinguish individual patches from patch matrices. Blue arrows indicate the angle of attack of the incoming flow. Panel (a) shows 10 distinct vegetation patches (green circles) and 10 distinct hydrodynamic patches (grey triangles). Panel (b) shows 10 individual vegetation patches and 1 hydrodynamic patch (dark grey triangle). Panel (c) shows 10 distinct vegetation patches and 1 hydrodynamic patch matrix because the different hydrodynamic 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
macrophyte patches; grey triangles indicate hydrodynamic patches (wakes) according to figure 3b; black areas indicate erosion patches (scour zones); black dashed lines indicate patches of low-flow favouring limnophilic macroinvertebrates such as *Asselus aquaticus*; white dashed lines indicate patches of high-flow favouring rheophilic macroinvertebrates such as *Rhitrogena germanica*. (b) Higher flow has a negative effect on the connectivity of the low-flow macroinvertebrates, but may cause stronger merging of the erosion patches with a positive effect on the connectivity of high-flow macroinvertebrates.