



# Biophysical Interactions in Fragmented Marine Canopies: Fundamental Processes, Consequences, and Upscaling

Andrew M. Folkard\*

Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom

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### \*Correspondence:

Andrew M. Folkard  
a.folkard@lancaster.ac.uk

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Spatial fragmentation is a near-ubiquitous characteristic of marine canopies. Biophysical interactions with fragmented canopies are multi-faceted and have many significant implications at multiple scales. The aims of this paper are to review research on biophysical interactions in fragmented marine canopies, identify current gaps in knowledge and understanding, and propose ways forward. The review starts at the patch/gap scale and focuses initially on hydrodynamic interactions. It then considers the consequences of these interactions for particulate and dissolved material, and distributions of canopy-associated organisms. Finally, it addresses issues of upscaling to landscape-scale and ways in which this research can be applied to marine landscape management. Work on a broad range of canopy types is considered, including micro-algal biofilms and turf algae; macro-algae, seagrasses and coral reefs; saltmarsh vegetation and mangroves. Although the focus is on marine canopies, insights from studies of fragmented canopies in other contexts are drawn on where relevant. These include freshwater environments and terrestrial forests, grasslands, crop canopies, and urban areas. Specific areas requiring greater attention are highlighted. As a result of this meta-analysis, the following recommendations are made for further research. A lack of basic data is identified across all canopy types regarding the formation, fate and spatial and temporal characteristics of canopy patches, gaps, and spatial structure. Studies of hydrodynamics with fragmented canopies would benefit from shifting focus toward more non-uniform, realistic configurations, while ecological research in this area would benefit from a move toward configurations that are more controlled and tractable for quantitative modeling. More comparative studies across canopy types would enable understanding of their biophysical interactions and their consequences to be more fully tested and developed. A greater incorporation of chemical aspects of canopy systems into work that has hitherto focused on biophysical interactions would also be pertinent. Upscaling of patch and gap-scale phenomena to landscape-scale is identified as a crucial topic, since it is at the latter scale that management efforts are most readily carried out. Overall, an approach that balances hydrodynamics, marine canopy ecology, spatial analysis of landscapes, biogeochemistry, and socio-environmental interactions is recommended.

**Keywords:** marine canopies, biophysical interactions, hydrodynamics, fragmentation, upscaling, patches, gaps

## INTRODUCTION

### Aims, Methods, and Structure

Spatial fragmentation – which can range from apparently random distributions to strongly-ordered patterning – is a near-ubiquitous characteristic of biotic and biogenic marine canopies (Thomson et al., 2012; Folkard and Bouma, 2016). It is found in both newly-developing and damaged canopies, as well as in established canopies in equilibrium with their surroundings. It can indicate healthy, resilient ecosystem functioning (Pringle and Tarnita, 2017) or stress and increasing – often anthropogenic – pressures (Fraschetti et al., 2012). The effects of interactions between hydrodynamic processes and fragmented canopies are complex, and dependent on a variety of biotic and abiotic factors. They are of fundamental importance to the structure, functioning and services of canopy ecosystems, since hydrodynamic processes are primary causes of (mechanical) stresses and facilitations (e.g., nutrient supply) to canopies and the ecosystems they support (e.g., Folkard, 2016). The hydrodynamics of fragmented canopies are more spatially heterogeneous than the hydrodynamics of homogeneous canopies – because of the spatial heterogeneity of the canopies themselves – and this leads to heterogeneity in their stresses and facilitations, e.g., spatial variations in sheltering (e.g., Folkard, 2005) and nutrient supply (e.g., Morris et al., 2008). Fragmentation of canopies also leads to their becoming more vulnerable to external pressures (Gera et al., 2013). Understanding the large-scale impacts these effects have is therefore important for managing the many coastal areas where marine canopies are found, especially those affected by anthropogenic stresses and climate change (El Allaoui et al., 2016).

The term ‘marine canopy’ can cover a wide range of types of bed cover. These have been studied with different emphases, according to the priorities and drivers of the research communities working on them. This paper brings together research on spatial canopy fragmentation and its interactions with physical processes (primarily hydrodynamics, but also sediment transport and other phenomena driven by hydrodynamics) from this wide range of canopy types. From this collation, it creates a structured synthesis of work in this field. From this, it compares approaches and progress in work focused on different canopy types to determine what can be learnt about each one, and to identify ways of developing more universal understanding. To perform this collation of literature, searches were carried out using Web of Science<sup>1</sup>. Searches were made for articles that included in their title, abstract or keywords: words beginning with “patch,” “gap,” “fragment” or “heterogen”; one or more canopy-type name (seagrass, seaweed, macrophyte, macroalgae, kelp, mangrove, saltmarsh, alga, biofilm, coral) or the word “canopy” or “canopies”; and one or more word referring to hydrodynamic processes (flow, current, wave, turbulence, hydrodynamics). For each word, wildcard asterisks were added to the end so that plurals and other related words would be found (e.g., turbulen\* was used to pick up turbulent, turbulence, turbulently etc.). This gave several thousand results, which were

then filtered by date (the last 10 years – since 2008, as the initial search was completed in 2018) and for papers before that date, by number of citations (selecting only those papers with > 50 citations). The cutoffs for date and citation number were chosen semi-arbitrarily to reduce the number of papers to a sufficiently large, but manageable amount. The resulting sample of several hundred papers were then filtered by subjective analysis of their titles and, in cases where this did not produce a clear decision, by reading their abstracts. The resulting list was checked to ensure that it included key papers from the author’s own knowledge of the literature. This resulted in a final set of approximately 300 papers on which this review was constructed, although not all of them survived the drafting process to appear in the final manuscript. Subsequently, smaller, more focused searches were used to identify papers on specific topics (approaches to habitat fragmentation in landscape ecology and flow-canopy interactions in terrestrial contexts) to fill gaps that arose in earlier drafts of the review. A small number (~10) papers recommended by reviewers have also been added to the final form of the manuscript.

The remainder of the paper is structured as follows. I begin, in the next section, by justifying my use of patches and gaps as the ‘unit elements’ of canopy fragmentation, and identifying the types of canopies to be covered. The following sections then lay out the structured synthesis of research across canopy types mentioned above. This starts from fundamental processes and works up to their consequences at landscape-scale for restoration and management. Thus, firstly, the causes, formation and evolution of individual canopy patches and gaps are reviewed. I then focus on the hydrodynamics of individual patches and gaps. This is followed by a section reviewing current knowledge of the consequences of these hydrodynamics-patch/gap interactions in terms of the transport and deposition of particulates and solutes, and the distribution of organisms. I then consider the upscaling of these consequences, firstly via studies of interactions between multiple patches and gaps, and then from a landscape-scale perspective. I then consider application of this work to marine canopy landscape restoration and management. Finally, I take a comparative overview of all this work, identify key research questions and recommend possible ways forward. Although the focus here is on marine benthic canopies, throughout, insights from studies of fragmented canopies heterogeneity in other contexts will be drawn upon where they provide relevant insights. These include freshwater lentic and lotic environments and terrestrial environments, including forest, grassland and crop canopies and urban areas.

## FRAMING: PATCHES, GAPS, AND CANOPY TYPES

### Characterization of Canopy Fragmentation in Terms of Patches and Gaps

The landscape-scale spatial structure of the sea floor in the coastal zone is often made up of patches of biota of various different sizes within a larger abiotic matrix (Robbins and Bell, 1994). The

<sup>1</sup><https://clarivate.com/products/web-of-science/>

inverse situation is also possible, in which the matrix made up of an approximately continuous biotic or biogenic canopy punctuated by gaps of relatively bare substrate or reduced canopy density (El Allaoui et al., 2016). Thus, these landscapes can be characterized spatially in terms of patches and gaps. There are many metrics associated with this perspective – for example, patch or gap size and density, edge length density (the mean length of canopy edge per unit area) – that have become widely used, particularly via earlier versions of the widely-used landscape ecology software package FRAGSTATS (McGarigal and Marks, 1995). As the field of landscape ecology has developed, alternative perspectives, in which fragmented landscapes are characterized by gradients, have been promoted (e.g., McGarigal and Cushman, 2005; McGarigal et al., 2009). More recently, there have been calls to re-think the conceptual foundations of landscape ecology, in light of better understanding of the non-linearity of relationships that determine the effects of fragmentation on ecosystems (e.g., Didham et al., 2012; Villard and Metzger, 2014; Liao et al., 2017). Thus, in some ways, research into canopy fragmentation has moved significantly beyond its characterization in terms of patches and gaps. Nevertheless, there are also many situations, where canopies are commonly organized into clearly delineated patches (e.g., salt marsh pioneer zones), or extended cover with clearly delineated gaps (e.g., seagrass meadows, mangroves). Therefore, the patch/gap conceptualization remains important. It also provides an idealized “unit element” of fragmentation for modeling studies of interactions between hydrodynamics and other physical processes, and fragmented canopies. Since this review starts from a focus on canopy-hydrodynamics interactions, therefore, it uses the patch/gap conceptualization.

This raises the question of how patches and gaps are defined. In many situations, this will be straightforward – as noted above, canopy patches and gaps are clearly delineated in many marine contexts. However, at times their edges are indistinct, and at others it is not clear whether a canopy distribution is a single but morphologically-complex patch, or a mosaic of several individual patches. For further discussion on this issue, the reader is directed toward Schoelynck et al. (2018). Hereinafter, I will assume that patch and gap edges are clearly defined.

## Canopy Typology

In a marine context, a range of benthic canopies may be identified. They can be distinguished from each other in many ways. Given that this review starts with canopy-hydrodynamics interactions, they are distinguished here in terms of the main parameters that govern these interactions, namely: (i) their height compared to the surrounding substrate and water depth; and (ii) the rigidity or flexibility of the canopy-forming organisms. The choice of what to include and exclude from this typology is, inevitably, somewhat subjective. Because the intention of the paper is comparative, the choice of canopy types is deliberately broad. Moreover, what constitutes a patch of canopy, and what is deemed the surrounding matrix depends on the scale of interest. Thus, for example, when studying seagrass meadows, the matrix of “bare substrate” surrounding patches of seagrass is typically covered by lower-growing organisms. But if the lower-growing

organisms are the community of interest, interest will focus on a smaller spatial scale, at which their vertical structure becomes relevant (e.g., Salta et al., 2013), and at which they can therefore be considered to be canopies. Hence, the smallest canopies included in this comparison are “micro-canopies” including micro-algal biofilms and turf algae. The second type of canopy is arguably the “classical” canopy, consisting of a permeable region whose elements rise significantly above the substrate. These include macro-algae beds, seagrass canopies and coral reefs. In the cases of macro-algae and seagrasses, these are made up of highly flexible elements, which pronate in the direction of flow, and oscillate back and forth in response to wave-forcing. The third category consists of pioneer saltmarsh vegetation but also includes pneumatophore roots of mangrove genera such as *Avicennia* and *Sonneratia*. These canopies are also permeable, but their elements tend to be more rigid than macro-algae and seagrasses. Moreover, they are found in inter-tidal regions, so that sometimes they fill the full water column depth and emerge above the water surface, while at others they may be fully submerged. Finally, mangrove genera with stilt roots such as *Rhizophora* form relatively rigid sub-aqueous canopies that are always emergent. Many of the areas of research reviewed herein are dominated by studies of one of these canopy categories, whereas others have been investigated in the context of several. Moreover, some of these types of canopy form patches or gaps more than others. For example, saltmarsh plants such as *Spartina anglica* typically form clearly defined patches in the pioneer zone, and canopy gaps are relatively common occurrences in seagrass meadows and mangroves. On the other hand, whilst coral reefs are highly spatially heterogeneous, they are not typically organized into clearly distinguished patches and gaps (Lowe and Falter, 2015). As a result, while there is an extensive literature on coral reef hydrodynamics (for reviews, see Monismith, 2007; Lowe and Falter, 2015), there is very little on the hydrodynamics of coral patches or gaps.

## PATCHES AND GAPS: FORMATION AND CAUSES

### Patches

Canopy patches are often found in areas that have been newly-colonized by the canopy-forming organism. The patches can grow from propagules or by clonal growth in clonal organisms such as seagrasses. Propagules can be dispersed widely, hence the creation of isolated patches. This dispersal can occur over very long distances, notably in seagrasses (Grech et al., 2016), and mangroves (Harwell and Orth, 2002).

Once they establish, the spatial structure of canopy patches is controlled by their growth strategy, which differs between species. For example, dense plant species can cause flow to deflect and accelerate around themselves, which militates against patch expansion because new shoots cannot survive in these faster flows. As a result, they tend to expand by releasing plant fragments which establish on bare substrate away from the parent patches and grow into new patches. On the other hand,

sparse species, which alter the flow less strongly, can grow more easily via expansion of existing patches (Verschoren, 2017). The distribution of patches is often affected by geology, topography and shelter from hydrodynamics stresses (e.g., energetic waves or strong tidal currents), although the underlying factor is usually access to sufficient nutrients and light (Koch, 2001). For example, Parnell (2015) found patches of giant kelp (*Macrocystis pyrifera*) and elk kelp (*Pelagophycus porra*) occurred preferentially on topographic highs, and Rinde et al. (2014) found that patches of the kelp *Laminaria hyperborea* established mainly on ridges. The higher elevation thus afforded to the kelp provides better access to water column nutrients and light. In contrast, Di Carlo et al. (2005) found that in shallow, well-lit waters, seagrass establishment was densest in topographic lows, because of the deeper layer of nutrient-rich sediment there. Similarly, Nardin et al. (2016) found that mangroves in a rapidly prograding area of the Mekong delta expanded as continuous coverage in areas of high sediment availability, but as sparse patches in areas of lower sediment supply. In both these cases, greater access to substrate nutrients is the determining factor. Patchy colonization may also be associated with preferential growth in areas where hydrodynamic stresses are lower, which may themselves be patchily distributed. For example, Francoeur et al. (1998) found that microform bed clusters provided refugia that allowed spatially-patchy establishment of periphyton in fast flowing rivers.

Canopy patchiness may also occur in post-disturbance areas, where canopies are damaged but recovering. The spatial pattern that this results in is affected by multiple factors. Underwood (1998) found that in an inter-tidal community of the macroalgae *Hormosira banksia*, post-storm patchiness was primarily caused by variations in the amount of damage sustained during the storm. Such recovery may also be subject to Allee effects (the weakening of individual plants' reproductive success with decreasing population density) leading to the canopy's accelerated decline, for example due to pollen limitation in sparse communities of intertidal *Zostera noltii*. This can impair their recovery even after environmental conditions have improved from those that caused their decline (van Tussenbroek et al., 2016).

As well as being indicative of newly-colonizing and post-disturbance canopies, patchiness can be a consequence of communities' spatial self-organization (Rietkerk and van de Koppel, 2008). This tends to result in pattern formation (Pringle and Tarnita, 2017), which can be complex and not just uniformly-spaced or -sized patches or stripes (van Wesenbeeck et al., 2008; van de Koppel et al., 2012). For example, it may be manifested as frequency distributions of patch size or separation distance which follow power law functions, i.e., where the probability that a patch's size (or distance from its nearest neighbor patch) is greater than some value  $s$  is proportional to  $s^{-\beta}$ , where  $\beta$  is a constant (Schoelynck et al., 2012). Spatial self-organization is defined as a process whereby large-scale ordered patterns emerge from disordered initial conditions due to small-scale interactions between organisms (Liu et al., 2014). It is generally considered to be due to scale-dependent feedbacks (Rietkerk and van de Koppel, 2008) – processes whereby

organism interactions change from positive to negative as spatial scale is varied. For example, pioneer salt marsh vegetation shoots grow together in patches for mutual protection and sediment and nutrient retention. But this causes flow to accelerate around them, causing increased substrate scouring which militates against shoots establishing within a certain distance of an established patch. Thus, near-field positive effects combined with far-field negative effects create patches (van Wesenbeeck et al., 2008). In other cases, the positive effect of nutrient retention by patches is counterbalanced by reducing light availability for each shoot as patches get larger (Gera et al., 2013).

## Gaps

Homogeneous canopies in which gaps may form tend to occur in regions where conditions are relatively uniform over wide areas, i.e., in the sub-tidal or in mangrove forests, rather than in transitional areas such as the inter-tidal, where canopies are often patchier. The main causes of gap formation include edaphic variations; damage or removal; burial and grazing. Edaphic variations result in canopy gaps where substrate is relatively poor or thin. Damage or removal can be due to natural forces – typically storms, but also mechanisms such as ice scouring (Cervin et al., 2004) – or anthropogenic causes, such as boat anchors, propellers, or infrastructure installation (e.g., Serrano et al., 2016). Likewise, burial can be caused by natural movements of bed material, usually during storms (Bell et al., 1999), or human activity such as deposition of dredging spoil. Herbivorous grazing can be relatively subtle, creating small scale mosaics of herbivore preferred and avoided patches, promoting plant biodiversity and resilience (Weerman et al., 2011; Howison et al., 2017), or more complete, leading to invasion by other species (e.g., Davies et al., 2007) or the creation of bioturbation pits (Yager et al., 1993). Grazing appears to be more important in some types of canopy (e.g., seagrass meadows, Townsend and Fonseca, 1998; Gera et al., 2013; periphyton biofilms, Gresens and Lowe, 1994; Holomuzki et al., 2006) than in others (e.g., macro-algae beds), although it may have a role in the persistence of gaps in the latter (Thomson et al., 2012). In some contexts, gap formation can be more complex. For example, in Argentinian salt marshes, Escapa et al. (2015) found salt pans formed gaps in *Sarcocornia*-dominated areas. They deduced that this was due to *Sarcocornia* growing in dense patches and providing shelter for crabs (*Neohelice granulata*). The crabs construct burrows, causing the *Sarcocornia* patch centers to die off. The patches then lose elevation relative to the surrounding marsh, and salt pans form within the depressions. Thus, the gaps are formed by interactions between biotic and abiotic processes.

Data on the extent, number and size of gaps in marine canopies is patchy. Bell et al. (1999) reported that gaps constituted 2.4–5.7% of a monospecific meadow of the seagrass *Halodule wrightii*. Gaps in algal canopies have been found to be larger at exposed sites than on sheltered coastlines, suggesting that a combination of exposure to external stresses and internal ecosystem context – e.g., canopy composition and grazing intensity – is fundamental to gap characteristics (Wernberg and Connell, 2008; Gera et al., 2013). Gap age appears to vary greatly. For example, Bell et al. (ibid.) found that most gaps in the

*Halodule wrightii* meadow they studied persisted for less than 6 months, whereas Thomson et al. (2012) inferred, from the ages of invertebrates within them, that gaps in the macroalgae canopies they studied had persisted for decades.

As is the case for patches, gaps are often in a dynamic state of evolution. Both seagrass (*Halodule wrightii*, Bell et al., 1999) and macroalgae (*Ascophyllum nodosum*, Cervin et al., 2004) canopy gaps have been observed to recover by re-growth or recruitment of the same species as the surrounding meadows. Jimenez-Ramos et al. (2017) noted that gaps and sparse areas of canopies have less self-shading, which should boost growth in them, homogenizing the canopy. Similarly, in a study of flow through seagrass meadow simulations made up of sparser and denser regions in various configurations, Adhitya et al. (2014) found that the flow tends to favor supply of water column resources to sparse areas, which may lead to homogeneity. In other cases, however, gaps are filled by other species. This can be caused by these invasive species being faster growing (e.g., Cervin et al., 2005) or having other advantageous species characteristics. For example, Vogt et al. (2012) observed that the regeneration of open patches after hurricanes in mangroves was dominated by flood-tolerant *Rhizophora*, which outcompeted the faster-growing, but less flood-tolerant pioneer *Laguncularia racemosa*, while Voerman et al. (2017) found that the ability of the invasive species *Caulerpa filiformis* to respond better to disturbance than native species allows it to outcompete them. Gap-filling mechanisms may also be affected by the clarity of gaps. For example, Wernberg and Connell (2008) found fucal algae to be recruited into complete clearings in a macroalgae canopy, whereas turf algae cover was more prominent in less complete clearings. The relative competitiveness of re-growth of meadow immediately surrounding a gap versus invasion into the gap from outside the meadow is likely affected by gap geometry and the permeability of its surrounding meadow. This determines whether flow arriving from through the canopy (favoring the surrounding meadow) or over the canopy (favoring invasion from outside) dominates within the gap (Folkard, 2016).

## HYDRODYNAMICS OF CANOPY PATCHES AND GAPS

Much work has been carried out in recent decades on the hydrodynamics of marine canopy patches, gaps, and their boundaries. Most of this work has been concerned with canopies of seagrass, saltmarsh plants or mangroves. These canopies are in many ways analogous to forest, crop or urban canopies in terrestrial settings, and much understanding has been developed by comparison of results from studies of aquatic and terrestrial canopies.

Significant contributions in this area have been made via analytical, numerical and physical modeling. The last of these has largely been carried out in laboratory flumes (or in wind tunnels for terrestrial canopies), often using artificial simulants – wooden dowels for rigid plants and plastic strips for flexible plants (see Thomas et al., 2014, for further discussion). These approaches are deliberately reductionist, the intention being to strip away

complexity and focus on quantitative, mechanistic understanding of specific biophysical interactions, with the subsequent aim of inferring their wider implications and thus moving toward greater understanding in a “bottom-up” way. They have also tended to focus on uni-directional currents, rather than on waves. There has, however, been significant recent progress in understanding wave interactions with homogeneous canopies through studies of simulated canopies representing a range of flexible and rigid vegetation (Pujol and Nepf, 2012; Pujol et al., 2013a,b) and canopies of seagrass (e.g., Zhang et al., 2018), saltmarsh vegetation (Moeller et al., 2014; Maza et al., 2015) and coral reefs (Lowe and Falter, 2015). Moreover, El Allaoui et al. (2015, 2016) have analyzed wave interactions with canopy gaps aligned both parallel and perpendicular to the wave direction.

Measurements of flow velocity – the essential form of hydrodynamic data – are analyzed by separating them into a mean flow field – the long-term average velocity at each location – and a turbulent field – the time-varying aspect of the velocity that remains when the mean velocity is subtracted from the time series of measured velocity. In biophysical terms, the impact of hydrodynamics on canopies can be divided into positive processes (supply of nutrients, dispersion of propagules etc.) and negative processes (e.g., physical stresses, which may lead to damage or uprooting). The mean flow and turbulence fields play different roles in these processes. Canopy organisms respond by adjusting their physiology and growth strategies, which in turn alter their impacts on the hydrodynamics. Thus, there arises a non-linear interaction between hydrodynamics and canopy biology. This rest of this section reviews recent work aimed at understanding these interactions at the single patch or gap scale. Historically, research in this area focused first on simpler, more idealized two-dimensional configurations, and then proceeded to more complex and realistic three-dimensional configurations. Therefore, the following exposition adopts the same distinction.

## Two-Dimensional Patch and Gap Simulations

The generic configuration under consideration here consists of a steady flow encounters a patch of a permeable canopy of obstacles with a uniform upstream edge. At the upstream edge of the patch, the flow adjusts to the presence of the canopy. If the canopy has non-negligible height and is permeable, it does this partly by flowing at an accelerated speed over the patch (the “overflow”) and partly by flowing at a slower rate through the patch (the “throughflow”). If the canopy is flexible, the flow causes it to pronate, thus the canopy also adjusts to the hydrodynamics. Belcher et al. (2003) provided an idealized model of this situation and identified three stages of adjustment. In the first, pressure due to canopy drag decelerates the flow in an impact region upstream of the canopy. The second region is an adjustment region that extends a distance  $L_C$  into the canopy. Here, flow decelerates until there is a local balance between downward turbulent transport of momentum from the overflow and removal of momentum by canopy drag forces.  $L_C$  is inversely proportional to the canopy density (the frontal area of canopy elements per unit bed area), so the extent of edge effects varies

with canopy structure (Peterson et al., 2004).  $L_C$  may be longer than the patch itself, so the flow doesn't reach equilibrium within the patch. Indeed, in highly fragmented landscapes, the flow may always be under the influence of canopy edges (Dupont et al., 2011). The third region is where the flow reaches equilibrium with the canopy. Here, the flow structure within the canopy depends on canopy density variations: in general, flow will be faster at heights at which the canopy structure is sparser. Depending on the height and density of the canopy, the flow above the canopy in this region may resemble either a mixing layer (denser canopies) or a boundary layer (sparser canopies) (Sukhodolova and Sukhodolov, 2012).

For patches of other types of canopy, the adjustment will be similar. Micro-canopies, in which through flow will be very small in comparison with the overflow, can be idealized for hydrodynamic purposes as changes in bed roughness with no significant change in bed height. In these conditions, the overflow will adjust to the different roughness characteristics of the patch compared to the surrounding substrate (Chamorro and Porte-Agel, 2009). This increases both the generation of turbulence and the bed shear stress. The former is generally advantageous to canopy organisms, since it increases the supply of nutrients through vertical turbulent diffusion. The latter is generally deleterious, since it increases mechanical stress, which can lead to physical damage or removal. For emergent canopies, only the throughflow will occur. Its mean flow and turbulent characteristics are determined by the size, spacing and frontal area density of the canopy elements (Nepf, 1999, 2012; James et al., 2004).

In terms of the turbulent flow field, enhanced turbulent energy is found close to leading canopy patch edges (Folkard, 2005). Similar effects are seen in wind fields at rural-urban transitions and upwind forest edges (Cheng and Porte-Agel, 2016). In emergent aquatic canopies, such as mangroves, this may be partly due to wave breaking, but also to turbulence generation in canopy element wakes (Norris et al., 2017). As the flow develops into the patch, the turbulence evolves. The sharp gradient in flow speed between the patch and its surroundings creates strong shear layers, in which coherent turbulent structures are generated (Siniscalchi et al., 2012). In a terrestrial context, Dupont and Brunet (2009) found that Kelvin-Helmholtz instabilities develop at the top of forest canopies, where there is a quasi-discontinuous change in the drag conditions between the region within the forest and the clear air above. As they move along the canopy, they roll over, then form transverse vortices. Secondary instabilities then destabilize these vortices, and by nine canopy heights downstream, they have become complex coherent structures. Submerged aquatic canopies have similar effects on the flow, but there are differences because of the finite depth of the water above the canopy. In aquatic contexts, the growth of the coherent structures stops when the production of the turbulent kinetic energy that feeds them in the shear layer at the top of the canopy is balanced by dissipation of that energy within the canopy (Ghisalberti and Nepf, 2004). These structures, and thus influence of the canopy overflow, penetrate a significant depth into the canopy, vertically dividing the canopy into an

upper region dominated by the overflow and a lower region dominated by throughflow (Nepf and Vivoni, 2000). These two layers often have very different flushing timescales, which can lead to their ecology and water quality also being different (Nepf and Ghisalberti, 2008).

Downstream of canopy patches in two-dimensional configurations, where the canopy edge geometry and flow velocity allow, recirculation zones form immediately behind the canopy which are similar to those found downstream of impermeable obstacles with a backward-facing step configuration (Detto et al., 2008). Whether this occurs or not, the shear layer at the top of the canopy extends downstream of the patch, forming a free shear layer "wake." In the wake, the turbulence increases first as the shear layer grows (the "near-wake"), then decreases as it decays (the "far-wake") (Folkard, 2005). At the same time, a new boundary layer starts to form above the bed downstream of the patch. As this grows, it comes to dominate the wake, which decays downstream. In the transition region from the canopy edge to the point where the wake is negligible and the bed boundary layer completely re-established, the flow structure is dynamic and multi-layered (Folkard and Bouma, 2016). This region often extends far downstream of the patch: Markfort et al. (2010) found that wind adjusting to a lake surface downstream of a tree canopy had reduced surface shear stress up to 50 canopy heights downwind of the transition, and in wind tunnel experiments, Markfort et al. (2014) found that mean turbulent quantities required at least 100 canopy heights to adjust to the new surface.

Less work has been done on the hydrodynamic influence of canopy gaps than on patches. Folkard (2011) compared flow in submerged canopy gaps to Morris's (1955) characterization of skimming flow, wake interference flow and isolated roughness flow, expanding the typology to five categories by separating wake interference flow into recirculation flow, boundary layer recovery, and canopy throughflow. He found that the type of flow that occurred could best be predicted using a Reynolds number based on overflow speed and gap depth, and the gap aspect ratio (i.e., the ratio of the gap length to its height). A Froude number based on the same speed and length scales was found to predict bed shear stress in the gaps well. Extending this work, Adhitya et al. (personal communication) found that longer leaves, lower shoot densities, deeper water and narrower gaps all led to dominance of throughflow over overflow in determining conditions in canopy gaps. In a study of wave interactions with canopies, Lowe et al. (2005) found that short wave orbital velocity is not significantly diminished in canopies compared to bare substrate, in contrast to canopies' significant attenuation of current velocities. As a result, Luhar et al. (2008) suggest that fragmented meadows are more likely to persist in current-dominated environments, because of the enhanced current feedback within canopy gaps, than in wave-dominated environments, where there will be a tendency toward homogeneity because of this lack of feedback. El Allaoui et al. (2015, 2016) reported flume experiments in which waves interacted with gaps aligned perpendicular and parallel to the wave direction, simulating sagittal channels that form perpendicular to coastlines in seagrass canopies due to

currents transporting waters mixed near the shoreline seaward. They found that, for both types of gap, wave velocity increased over the gap compared to the canopy and that denser canopies attenuated both wave velocity and turbulent kinetic energy within adjacent gaps, compared to sparser canopies. Modeling based on these results showed that, for the same total gap area, canopies with large gaps cause more mixing than canopies with small gaps.

### Three-Dimensional Patch and Gap Simulations

As computer power and physical modeling facilities have developed, more hydrodynamic studies of three-dimensional patches have been carried out, although to date, there appear to have been no three-dimensional studies of canopy gap hydrodynamics. Most commonly, 3D patch experiments have used idealized, circular patches made up of uniform elements. The flow is diverted around their sides, as well as flowing over and through them. Horseshoe or necklace vortices form around the upstream patch edge (Chang and Constantinescu, 2015; Chang et al., 2017). The flow accelerates as it moves around the patch, the lateral distance from the patch where maximum flow occurs increasing with patch size (Vandenbruwaene et al., 2011). As at the top of the canopy, there is a strong velocity gradient across the lateral patch edges, causing coherent horizontal vortices to form (Yan et al., 2016). These enhance lateral transport across the patch edges (Zong and Nepf, 2011).

Downstream of three-dimensional patches, the wake structure is complicated in comparison to the two-dimensional case by the convergence of the flow around the patch with the overflow and throughflow. For dense patches where overflow dominates throughflow, the patch width-height ratio determines the orientation of wake vortices. If the height is less than the width, vortices form in the vertical plane within a few patch heights downstream of the patch. If the height is greater than the width, horizontal vortices form closest to the patch and control velocity recovery within the wake (Liu et al., 2018). In cases where the throughflow is significant compared to the overflow, there are two peaks of turbulent intensity behind a circular patch. The first is directly behind the patch and related to the wakes of the individual patch elements. The second is further downstream and related to the patch-scale wake (Chen et al., 2012; Chang and Constantinescu, 2015). As patches narrow, the horizontal shear layer becomes more important and there is a mix of horizontal and vertical shear layers, so wake recovery is slower (Chen et al., 2013).

## CONSEQUENCES OF HYDRODYNAMIC INTERACTIONS WITH CANOPY PATCHES AND GAPS

### Mineral and Organic Particulates

An important consequence of the hydrodynamic influences of canopy patches is their effects on sediment resuspension, transport and deposition. This involves highly non-linear

interactions, since each element of the hydrodynamics-canopy-sediment triad influences the others. Enhanced sediment deposition creates new substrate, which provides nutrients and anchoring, encouraging enhanced canopy growth, and this positive feedback maintains spatial correlation between canopy and substrate distributions (Baatrup-Pedersen and Riis, 1999). Sediment resuspension reduces light levels, which reduce canopy growth rates, leading to sparser canopies, enabling further resuspension (Adams et al., 2016). Resuspension can occur because of enhanced turbulence or enhanced mean flow – thus sediment may be resuspended within patches even if mean flow speeds are below the threshold of sediment motion, due to stem wake turbulence (Lefebvre et al., 2010). Conversely, sediment deposition within patches may only be enhanced in the absence of stem wake turbulence (Liu and Nepf, 2016). Patches generally have two sources of sediment – from upstream and laterally. The relative contributions of each determine the spatial pattern of in-patch deposition (Zong and Nepf, 2011). Where advection from upstream dominates, net deposition initially increases as flow decelerates on entering a patch, then decreases as suspended sediment concentration decreases (Zong and Nepf, 2010), so there is a point of maximum sedimentation at some distance into a patch.

Sedimentation downstream of circular patches varies depending on the rigidity and density of the patch elements. For rigid elements, the patch throughflow shifts the patch-scale wake downstream, so there is a region of relatively stagnant flow and thus enhanced deposition immediately downstream of the patch (Chen et al., 2012). For flexible elements, the flow adjustment is more three-dimensional, and turbulence is enhanced immediately downstream of the patch so deposition is reduced there (Ortiz et al., 2013). In sparse patches of rigid elements, sediment is scoured from within the patch and deposited closer downstream than that from denser patches, because the latter divert flow more (Follett and Nepf, 2012). The spatial pattern of sediment deposition around and downstream of a circular patch of model vegetation varies primarily with the ratio of shear velocity to critical shear velocity. If this is  $< 0.7$ , there is high deposition in both the wake and adjacent zones. If it is  $0.7-3$ , deposition is high in the wake only. If it is  $> 3$ , deposition is low everywhere. The deposition pattern correlates better with shear velocity than with settling velocity, implying that the patterns are driven by resuspension, not deposition (Shi et al., 2016). Again, there have been very few similar studies of the sedimentary consequences of canopy gap hydrodynamics, although Folkard (2011) provides some speculative inferences from a purely hydrodynamic flume study.

These effects in mineral particles are important, since they provide nutrients to canopy organisms and scale-up to affect landscape-scale geomorphology. Of greater importance ecologically, the influence on hydrodynamics of canopy patches and gaps also affects organic particles – including food, waste material, reproductive propagules and plankton. In transport, organic particles behave physically in many ways like mineral sediments. However, the timing of release of organic particles is governed by organism biology, and their deposition is governed by their varying buoyancy and morphology (Gurnell, 2007).

Therefore, the behavior of organic particles is more complex than that of mineral particles, so these complexities need to be taken into account in their modeling.

## Solutes

Because of their influence on fluxes and budgets of solutes, aquatic canopies are important in determining the biogeochemistry of water bodies (Bal et al., 2013) and canopy fragmentation can have a significant effect on this. Canopy organisms can take up nutrients from the water column or, if they are rooted, from the substrate. Canopies of plants can also provide substrate for epiphytic biofilms, which also take up nutrients (Levi et al., 2015). Spatial patterns of in-canopy flow are highly correlated with solute uptake rates, which are enhanced by up to 20% at the leading edges of canopies (Morris et al., 2008; Bal et al., 2013). The hydrodynamic effects of seagrass canopy leading edges also drives nutrient exchange between the water column and the substrate; this is caused by pressure gradients arising from flow deceleration (Adhitya et al., 2016). Canopy patches often concentrate and store dissolved nutrients (Schoelynck et al., 2012). Tussocks of wetland sedges efficiently retain biogenic silica, giving them a competitive advantage (Opdekamp et al., 2012). In the Okavango delta, aquatic macrophytes accumulate and concentrate organic matter in sediments below patches, allowing high productivity in an otherwise oligotrophic environment (Schoelynck et al., 2017). Liu et al. (2017) also found this 'soil island' effect around isolated and clustered tamarisk (*Tamarix chinensis* Lour.) in a coastal wetland. However, the effect size was less for clustered tamarisks than for isolated ones, implying that the effect will be weakened by vegetation restoration or natural expansion. Solute retention can vary within patches: Hemminga et al. (1998) found that growth at *Spartina anglica* patch edges was dependent on nutrients in the local substrate, whereas in the (older) patch centers, this material had been depleted in previous years, and growth depended on nutrients bound to allochthonous organic particles.

## Distribution of Canopy-Dwelling Organisms

Patch and gap interiors and edges can be very different environments, and strong gradients can exist in both environmental and canopy parameters across patches and gaps. This can alter ecological interactions even within single patches or gaps (Mota et al., 2015). In biological terms, differences between edges and interiors are found in the properties of the canopy-forming organism itself (e.g., Brun et al., 2003); in faunal abundances (e.g., Barbera-Cebrian et al., 2002; Bologna and Heck, 2002; Efirid and Konar, 2014); in the levels of thermal (Jurgens and Gaylord, 2016) and mechanical (Folkard, 2005) stresses experienced by organisms; and in terms of sediment quality (e.g., Alves et al., 2017). Local diversity and distribution of benthic fauna is intimately associated with canopy type and distribution (e.g., Begin et al., 2004; Bouma et al., 2009). Macrophyte structural complexity plays an important role in determining differences in macroinvertebrate distribution

between canopies of different species (O'Hare and Murphy, 1999). This is likely driven by differences in hydrodynamic stress attenuation and food availability rather than structural complexity *per se* (Bell et al., 2013). Canopies of macroalgae with greater structural complexity also promote spatial and temporal patchiness of microphytobenthos, with potential significant effects on the overall productivity of ecosystems (Umanzor et al., 2017). Fragmentation of seagrass canopies also alters their interactions with filter feeders. Within canopy patches, filter feeders' food supply is reduced, strongly restricting their growth (Reusch and Williams, 1999), but in the gaps between canopies, they can find greater protection from hydrodynamic forces and higher resource availability (Gonzalez-Ortiz et al., 2014). Thus the fragmentation allows the seagrass and filter feeders to co-exist compatibly.

## UPSCALING TO LANDSCAPE-SCALE

An important aim of studies of fragmented canopies is to be able to quantify total or average parameter values at the whole-landscape scale. Whilst these require knowledge of inputs and characteristics at that scale, they also require understanding of structure and processes at smaller scales, i.e., patch and gap-scale. In part, this is born of necessity, since field measurements are generally made at patch and gap scales for logistical reasons, so landscape-scale measurements tend to have to be derived from their upscaling. Moreover, variability at patch and gap scale within fragmented canopies often has important effects on landscape-scale structures and processes, and this has given rise to many different approaches to upscaling (e.g., Bou-Zeid et al., 2004; Chesson et al., 2005; Denny and Gaylord, 2010; Nikora, 2010).

If parameters of interest scaled linearly with spatial scale, upscaling would be trivial – it would simply comprise of adding up the contributions of each patch or gap-scale area to give a total for a whole landscape. However, this is not the case. Most, if not all, parameters of interest in aquatic canopy ecosystems scale non-linearly with spatial scale (Chesson et al., 2005). In addition, emergent forms and processes often arise at larger scales that are not apparent at the individual patch or gap scale, due to the spatial distribution of patches and gaps. For example, the spatial density and distribution of patch or gap edges plays a large part in governing landscape-scale flow structure (Dupont et al., 2011; Folkard and Bouma, 2016), and in saltmarshes, regions of relatively dense vegetation deflect flow into more sparsely-vegetated regions, where drainage channels form. Thus, landscape-scale drainage rates are determined in part by the spatial distribution of vegetation patches (Temmerman et al., 2007; Vandenbruwaene et al., 2013). These issues provide the main challenges in upscaling of patch and gap-scale phenomena to enable derivation of landscape-scale parameter values.

These challenges are addressed in two general ways. Empirically, correlations can be sought between variations in metrics describing the patch/gap-scale structure of fragmented



canopy landscapes and variations in landscape-scale total or average parameter values. While this approach can provide evidence of these cross-scale relationships, they do little to provide causal, mechanistic insights to them. The alternative approach is to create spatially-distributed models into which the smaller scale processes are explicitly incorporated but which operate over domains covering entire landscapes. These can then be explored to elicit mechanistic understanding of the cross-scale relationships. They can also be used to infer correlative relationships between patch/gap-scale causes and landscape-scale effects of the type described above that are underpinned by that mechanistic understanding (e.g., Luhar and Nepf, 2013; Larsen et al., 2017). However, such models require detailed understanding, not only of the nature of processes at the smaller scale, but also of ways in which these interact with each other as spatial complexity and scale are increased. Therefore, there is a need for studies of these interactions and the ways in which they influence landscape-scale phenomena, as well as for development of robust and broadly-applicable techniques for their upscaling.

An ecological perspective on the problem of non-linearity in upscaling can be illustrated by the example of trying to estimate the growth rate of a canopy from knowledge of the percentage of algal cover. Because increased algal cover enhances algal growth rate due to mutual protection effects at the patch scale, applying the patch-scale relationship to calculate growth rate from percentage cover at landscape-scale will not give an accurate value. To address this type of problem, scale transition theory (Chesson et al., 2005; Benedetti-Cecchi et al., 2012; Chesson, 2012) quantifies the non-linear scale-dependence of interactions between parameters in terms of the variances and co-variances of their patch/gap-scale values across whole landscapes. Larsen et al. (2017) provide an illustration of how the problems of non-linearity and spatial distribution effects in upscaling are addressed in a hydrological context in a study of the flow through the vegetated ridge-and-slough landscape of the Florida Everglades. Following approaches that have been used previously in the groundwater literature (Cushman et al., 2002; Farmer, 2002), they calculate the landscape-scale average flow resistance as a non-linear spatial average of small scale roughness, using an approach based on the ergodic hypothesis (Lumley and Panofsky, 1964). They conceptualize the landscape as binary – being made up purely of patches and gaps of ‘matrix’ between them. The landscape-scale average of a parameter (flow resistance in the case of Larsen et al., 2017),  $H_{\text{land}}$ , is then calculated from values of the same parameter for the patches,  $h_p$ , and the gaps,  $h_g$ , and the fractional cover of patches,  $p$ , across the whole landscape as

$$H_{\text{land}} = [ph_p^\omega + (1 - p)h_g^\omega]^{1/\omega} \quad (1)$$

The non-linearity and dependence on spatial distribution are incorporated in the exponent  $\omega$ , which is calculated by fitting the data produced by repeat runs of a numerical model of the landscape, based on long-term field observations (see Larsen et al., 2017, for further details). They then, via this model, explore the dependence of  $\omega$  on changes in various metrics describing the heterogeneity of the landscape.

In order to be able to test and develop upscaling approaches such as scale transition theory and non-linear spatial averaging, understanding is needed of ways in which all aspects of canopy ecosystems interact as spatial complexity and scale increase. The remainder of this section identifies progress that has been made in understanding these interactions, firstly via studies of interactions between two or more patches or gaps. It then covers interactions between patch-scale and landscape-scale processes, and finally identifies some landscape-scale consequences of these interactions in fragmented canopies. Because work in this area to date is at a relatively early stage of development, the coverage is necessarily illustrative, rather than comprehensive.

## Hydrodynamically-Mediated Interactions Between Canopy Patches

Taking a bottom-up approach, the first stage in understanding how processes at patch/gap-scale scale up is consideration of the interactions between two patches or gaps. In an aquatic context, hydrodynamics is usually the dominant mediator in these interactions. For example, where a downstream patch is located in the hydrodynamic wake of an upstream patch, the wake's enhanced turbulence will alter the conditions in the downstream patch (Folkard, 2005). This can affect its nutrient uptake rate, due to changes in both the mean flow speed and the levels of turbulence (Cornacchia, 2018). Other interactions will involve hydrodynamically-mediated sediment processes. For example, when the two side-by-side patches are far apart, their wake interactions are weak, and each has its own region of sediment deposition behind it. If the transverse distance between them reduces, their wakes will start to interact and a depositional region will form further downstream where their wakes merge (Meire et al., 2014). This encourages formation of a new vegetation patch, which will slow the flow between the patches and allow them to merge (de Lima et al., 2015; Liu et al., 2018). Over time, this process may lead to continuous vegetation coverage (Kondziolka and Nepf, 2014). Because of the differences in their interactions with flow, these morphological feedbacks will be different for rigid and flexible vegetation (Ortiz et al., 2013). This leads to a different set of outcomes when patches of different species interact. For example, Cornacchia et al. (2019) found that when a patch of a vegetation species with a taller, denser canopy (*Callitriche*) was located upstream of a patch of a shorter, sparser species (*Groenlandia*), it generated a turbulent wake that enhanced nutrient uptake by the *Groenlandia*. At the same time, the uptake rate of the *Callitriche* benefited from being exposed to the higher mean velocity of the upstream flow, as its canopy was too dense for turbulence to penetrate.

## Influence of Canopy Patch Interactions at Landscape-Scale

Interactions between canopy patches, hydrodynamics and sediment processes of the type described in the previous section can lead to landscape-scale structure in the spatial distribution of canopies. For example, in saltmarshes, regions of relatively dense vegetation can deflect flow into more sparsely-vegetated

regions, leading to preferential formation of drainage channels in the latter. As a result, the saltmarshes evolve with some regions characterized by dense vegetation, and others by drainage creek networks (Temmerman et al., 2007; Vandenbruwaene et al., 2013). Other examples of feedbacks between vegetation canopies, flow and sediment processes governing the evolution of landscapes have been found by Larsen et al. (2007) and Larsen and Harvey (2010, 2011) in studies of the ridge-and-slough patterning of vegetation distributions in the Florida Everglades.

In forming these spatial structures, ecological traits of the canopy species are often important. For example, rate of growth is an important determinant of canopy patches' contributions to landscape dynamics (Bertoldi et al., 2011). Where patches grow fast, they are more resilient due to their ability to recover from disturbance more quickly. Slower growing species also tend to decline more slowly, so are resistant to degradation (O'Brien et al., 2018). These differences will lead to differences in the evolution of canopy-hydrodynamics-sediment interactions and thus differences in spatial structure. Variations in establishment strategies amongst canopy-forming species (e.g., clonal extension, ruderal gap filling), variable spatial and temporal patterns of disturbance (van Hulzen et al., 2006), and the extent to which they change their physical structure and biomechanical properties over their growth-senescence cycles (Kleeberg et al., 2010) will also significantly modify their landscape-forming function. In general, canopy species' role in landscape dynamics is to act as ecosystem engineers (Jones et al., 1994) – they trap and stabilize sediments, organic matter and propagules of other species, modify local sediment and morphology, and drive development of landforms and habitats (Gurnell, 2007; Gurnell et al., 2012). Aboveground biomass modifies flow and retains sediment, while below ground biomass affects the hydraulics and mechanical properties of the substrate. Thus, their effects change as above and below ground biomass fractions change in response to climatic and hydrodynamic forcing (Gurnell, 2014).

The upscaled consequences of patch-scale interactions will also often interact with larger scale processes. Generally, the large-scale processes determine the overall extent of the fragmented canopy and can shape and orient the patches and gaps in the landscape, while small-scale interactions generate the patch/gap-scale structure (van de Koppel et al., 2012). For example, Fonseca et al. (2008) found that the spatial organization of *Halophila decipiens* (Caribbean seagrass) in an open ocean setting subject to hurricane damage was dictated first by large scale dispersal of propagules (over 100s of meters) then, within a growing season, by clonal organization of individual seagrass patches. The large-scale controls can include anthropogenic disturbance: in the Wadden Sea in NW Europe, the landscape-scale consequences of increased human disturbance of sediment (e.g., dredging of navigation channels and ports) has interfered with biological controls of sediment dynamics and have shifted the inter-tidal zone from a state of internal regulation (by the ecosystems within the zone) and spatial heterogeneity to external regulation (by anthropogenic impacts originating outside the zone) and spatially homogeneity (Eriksson et al., 2010).

## Consequences of Patch-Scale Interactions at Landscape-Scale

Understanding of the landscape-scale consequences of interactions between canopy patches, hydrodynamics and hydrodynamically-mediated sediment processes is mainly focused on those particular elements of the ecosystem (i.e., the patches, hydrodynamics and sediment themselves). However, there have also been some studies of their influences on some of other physical, chemical and biological aspects of fragmented canopy ecosystems. For example, they have an important influence on solute diffusion coefficients and residence times (Nepf et al., 1997; Nepf, 1999). These can vary by an order of magnitude across fragmented canopies because of the great difference in flow speed between canopy throughflow, and flow over and around patches (Lightbody et al., 2008). This can affect the canopies themselves, for example by varying their exposure to pollution or their access to dissolved nutrients and gasses (Lara et al., 2012).

Another major landscape-scale ecological consequences of interactions between hydrodynamics and fragmented canopies is their effect on habitat diversity. However, the nature and direction of these effects (i.e., whether they increase or decrease habitat diversity, or leave it unchanged whilst changing the mix of habitats) remains unclear. The heterogeneous flow conditions created by fragmented canopies create a highly diverse mosaic of habitats (Sukhodolov and Sukhodolova, 2010; Verschoren, 2017). According to the long-established patch dynamics concept, high levels of spatial habitat variability imply high levels of species richness (Townsend, 1989). However, this is not always well-supported by data (Resh et al., 1994). In a meta-analysis of seagrass research, neither literature review nor field measurements suggested that habitat fragmentation has any consistent effect on fauna, and there was little evidence of fragmentation sensitivity in any taxonomic group (Bell et al., 2001). Lefcheck et al. (2016) found that abundance, species richness, Simpson and functional diversity and composition of faunal communities were invariant to fragmentation in experimental eelgrass landscapes. They concluded that this is likely a consequence of the fauna's rapid life histories and high mobility. In other studies, however, such relationships have been found: Matias et al. (2015) found that higher habitat complexity in fragmented macro-algae canopies promoted species colonization, so the higher the level of fragmentation, the more species were present. Thus, the relationship between hydrodynamic interactions with fragmented canopies and species richness of communities inhabiting those canopies requires further investigation.

## APPLICATIONS TO MARINE CANOPY LANDSCAPE MANAGEMENT AND RESTORATION

As noted by Bell et al. (1997), there is a powerful mutualistic relationship between the practice of landscape restoration and the science of landscape ecology. Restoration can provide

experimental spatial distributions and opportunities for experiments over large spatial scales. Landscape ecology can provide insights into selecting reference sites and establishing restoration project goals, and appropriate spatial configurations to aim for. The same kind of mutualistic relationship is also evident between the practice of river restoration and the science of eco-hydromorphology and eco-hydraulics, which focus on interactions between ecology, catchment hydrology, river channel hydraulics and channel and floodplain geomorphology (e.g., Vaughan et al., 2009). Similar mutually beneficial links exist between the practices of coastal zone restoration, protection and management, and the science of biophysical (and chemical) interactions in coastal marine ecosystems – many of which have canopy organisms as keystone species. Some examples of ways in which understanding of canopy spatial distribution and fragmentation can be utilized in coastal zone management are given below.

Analysis of canopies' spatial distributions can be used effectively to describe the impacts of multiple human stressors in marine environments (Tamburello et al., 2012). van der Heide et al. (2010) found consistent responses of spatially self-organized patterns in seagrass meadows to changing abiotic conditions, and suggested that this could lead to the use of self-organized spatial patterns as stress indicators in these meadows. Even in inter-tidal diatom micro-canopies, spatial patterns can provide important clues about level of degradation of ecosystem (Weerman et al., 2012). However, interpretation of these patterns requires detailed knowledge of the nature of underlying feedbacks, including hydrodynamically-mediated feedbacks, as the patterns differ markedly between ecosystems. Of potentially greater value, understanding of the spatial distribution of canopy fragmentation can be used to predict the development of canopies and identify those that are at risk of catastrophic decline (Rietkerk et al., 2004). For example, the shape of *Spartina anglica* patches has been found to indicate the long-term development of salt-marsh pioneer zones, although the outcome is conditional on large scale morphodynamics and sediment grain size (Balke et al., 2012). Frascchetti et al. (2012) suggested that increasing spatial heterogeneity of both intertidal and subtidal assemblages probably represents an early warning of increasing human pressure in marine protected areas. In a model of seagrass meadow spatial patterning, Ruiz-Reynés et al. (2017) found that a transition to patches of vegetation arranged in approximately hexagonal formations indicates that the meadow is close to a tipping point where further increase in mortality may lead to catastrophic loss of the meadow.

Fragmentation of canopies at landscape-scales may also be used as a bio-indicator of loss of abundance amongst canopy-using organisms. For example, properties of fragmented landscapes at 10–100 m scales have been found to be effective indicators of nekton distributions, with lower nekton abundances correlating with higher degrees of canopy fragmentation and loss of habitat connectivity (Baillie et al., 2015; Favre-Bac et al., 2017).

Better understanding of the hydrodynamics of canopies at patch/gap and landscape-scales may also help attempts to re-establish or restore marine canopies. Attempts to re-seed

and re-turf seagrass canopies have been made in marine environments but have had limited success (van Katwijk and Hermus, 2000; van Katwijk et al., 2009). Natural re-establishment of macrophyte patches has been somewhat more successful in streams (Larned et al., 2006). In these environments, the main bottleneck for re-colonization is the initial establishment of attached roots in the sediment from propagules or seedlings (Riis, 2008), therefore understanding of the hydrodynamic conditions that facilitate this process for different canopy types in different contexts would be valuable. Once they have established, patches of plant canopy are able to create interactions with the flow, leading to positive feedback that causes enhanced sediment deposition and allows the patches to expand (Sand-Jensen, 1998).

## COMPARISON ACROSS CANOPY TYPES AND PROPOSED DIRECTIONS FOR RESEARCH

Having provided a structured synthesis of work on biophysical interactions with a wide range of canopy types in the preceding sections, this final section compares the approaches taken and progress made in work focused on different canopy types, and draws out what can be learnt about each one, and how we can develop more universal understanding of these interactions, their consequences and how they can be harnessed for management purposes.

In terms of patches and gaps themselves there appears to be a lack of basic data across all canopy types regarding how commonly they occur; their size, shape and orientation distributions; and how long they typically persist. This sort of information is important, as it allows models predicting their evolution and consequences to be developed on the basis of realistic data. Comparative studies of the modes of formation, maintenance and destruction of patches and gaps across different canopy types might also help to elucidate the relative importance of different factors (environmental gradients, biotic and abiotic stresses and facilitations, catastrophic events) for each one.

The study of fundamental hydrodynamic interactions with canopies has largely been carried out via laboratory flume or basin studies, numerical modeling and field experiments. These have typically used more-or-less idealized hydrodynamics (uniform flows or wave fields) and canopies in simplified two- or three-dimensional configurations. Often, the elements of the canopies have been idealized using simulants, which are uniformly rigid (e.g., wooden dowels) or flexible (e.g., plastic strips). These simulations have tended to be based on the essential biomechanical and morphological properties of seagrasses, saltmarsh vegetation, and mangroves. From this, a relatively detailed and thorough understanding of the hydrodynamics of these types of canopies has been built up. The review carried out suggests that less work has been done on the fundamental hydrodynamics of lower growing organisms – biofilms, turf algae etc. Moreover, the strongly reductionist, idealizing approach taken in this work to date suggests that moves toward greater realism in these experiments is needed. For example, this

would include studies of the hydrodynamics of patches or gaps with boundaries that are not quasi-discontinuous, which vary in height and density, and which have elements with variable morphology. Studies incorporating a wider range of configurations of patches and gaps – for example cases in which patch-gap edges are aligned at intermediate angles to the direction of the oncoming current or waves (rather than being parallel or perpendicular to it, as has almost universally been the case hitherto), or where edges are not either straight or circular – and less uniform hydrodynamic conditions might also elucidate non-linear interactions between variations in canopy and hydrodynamic characteristics.

Studies of the effects of hydrodynamic interactions with canopy patches and gaps on particulates, solutes and canopy-dwelling organisms appear from this review to have focused mainly on canopies of seagrasses, saltmarsh vegetation, macroalgae, and mangroves. This suggests that there is a need for further work in this area on low-growing canopies, where the focus hitherto appears to have been more biological (e.g., on patterns of grazing) than hydrodynamic. In general, as with studies of the hydrodynamic interactions with canopies, the physical aspects of this topic appear to have been studied largely through idealized configurations, whereas the biological aspects have been mainly studied through field measurements of *in situ* ecosystems. Moving the former toward more complex, realistic settings, and the latter toward more controlled focused conditions will help to bring understanding of biophysical interactions in these contexts from biological and physical perspectives closer together.

Arguably the most consequential motivation for studying these interactions is a desire to be able to predict how marine canopy landscapes will be affected by our actions, and how they can help us via their ecosystem services. This ability would enable us to guide our actions and harnessing of those services. This implies that landscape-scale is the scale at which the insights delivered by research may be applied most usefully. This is at odds with the fact that the most common scale for measurement and modeling – due to logistical and technological limitations – is the patch/gap scale. Therefore, upscaling from patch/gap scale to landscape-scale is arguably the most important current problem in fragmented marine canopy research. Although significant progress has been made in this area in recent years there still remains much to be done. Further studies are needed into the mechanics of interactions between multiple canopy patches and gaps at all scales – from interactions between two patches, through studies of patch mosaics (Schoelynck et al., 2018) and fragmented canopies with more complex spatial distributions, to whole-landscape scales. These need to take into account the roles of a wide range of different variables, including those related to hydrodynamics (waves, currents, turbulent mixing), sediment (erosion, resuspension, transport, deposition), and other physical variables such as light levels (e.g., Koch, 2001; Adams et al., 2016) and water temperature. From a chemical perspective, they need to include concentrations of nutrients, dissolved gasses, pollutants and a wide range of biogenic chemicals, as well as

their flux rates, both in terms of physical movement between the substrate, water column, biota and atmosphere, and in terms of chemical changes, for example from dissolved to particulate form, or organic to inorganic form. From a biological perspective, they need to include rates of primary production, bulk biomass, species diversity and richness, and metrics of ecosystem structure, functioning and services. Clearly, no single study or model could incorporate all of these variables. They are listed here to emphasize the importance of considering the full range of factors that may be at play in determining the dynamics of fragmented marine canopies.

In summary, a number of general ways of progressing the science driving our ability to manage ecosystems and landscapes characterized by fragmented marine canopies approaches can be identified. Firstly, closer collaboration is required between researchers carrying out work aimed at improving our understanding of the fundamental processes of biophysical interactions with fragmented canopies, practitioners of landscape management and restoration, and policymakers concerned with coastal environments. Within the research community, traditionally reductionist, laboratory and numerical model-based hydrodynamics research would benefit from a move toward studying more non-uniform, varied and realistic configurations, and traditionally holistic, field-based ecological research would benefit from a move toward studying more controlled, idealized and quantitatively-modelable configurations. Moreover, a greater appreciation of the importance of chemical aspects of the systems studied needs to be incorporated into the current biophysical approach. Further development of techniques for upscaling understanding and predictions of bio-chemo-physical interactions at the patch/gap scale to the landscape-scale in the context of spatially complex canopies is required. All of these would benefit greatly from a globally distributed experiment approach (Borer et al., 2014) with a clear shared direction and aims. Finally, in attempting to interweave the fields of hydrodynamics, marine canopy ecology and spatial analysis of landscapes, whilst incorporating biogeochemistry and socio-environmental interactions, an approach that balances these disciplines, rather than viewing one as subordinately serving the other, would be the best way forward.

## AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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