

CREATING PATCHES OF COMPREHENSION AND FILLING GAPS IN KNOWLEDGE: PHYSICAL MODELLING CONTRIBUTIONS TO JOINED-UP UNDERSTANDING OF HETEROGENEOUS ECO-SCAPES

ANDREW FOLKARD

Lancaster Environment Centre, Lancaster University

Lancaster, LA1 4YQ, United Kingdom

Most “eco-scapes” (by which I mean spatial distributions of ecosystems), including those in aquatic environments, are heterogeneous, a condition which can be indicative of a healthy, resilient diversity of habitats, or of fragmentation, stress and decay. This heterogeneity is often conceptualised in terms of “patches” and “gaps”, amongst other spatial elements. Interactions between the ambient hydrodynamics and patches and gaps in organism distributions are therefore central to determining ecosystems’ structure, functioning, possible future trajectories and responses to anthropogenic interventions. This paper will review work carried out over the past few years aimed at understanding these interactions and their implications, which has used physical modelling as its primary *modus operandi*. The key findings of this work are that the nature and density of gap-patch boundaries, and the relative locations of patches and patch-wakes, are of overriding importance in determining how the organisms and hydrodynamics influence each other and the morphological, sedimentary and biogeochemical aspects of their wider environments. This paper discusses these issues using examples from studies of two keystone coastal organisms, seagrasses and mussels, and suggests ways in which research in this area might best try to proceed.

1 INTRODUCTION

Pattern formation and spatial heterogeneity are common in many ecosystems, and indeed an entire field of research – spatial ecology – has evolved to study the nature of these spatial patterns and their relationships to ecosystem form and functioning [17]. To a large extent, the observed spatial distributions of ecosystems are the result of organisms’ self-organization in response to external, biotic and abiotic conditions [5]. These conditions may be facilitative (for example, the provision of food, shelter or sanctuary from predators) or stressful (for example, the application of potentially damaging physical forces, predation or scarcity of food or water). In most, if not all, natural situations, both of these types of conditions are present, and act at multiple spatial scales, resulting in a complex set of actions and interactions which can, nevertheless, result in clear spatial structuring of ecosystems [27].

The physical characteristics of ecosystems – specifically benthic ecosystems in aquatic environments – are of interest to hydraulicians since they usually change the bed roughness, and thus contribute to the governance of the nature of flow and wave fields that pass over them [16]. Moreover, these ecohydraulic interactions affect sediment fluxes and can have a strong influence on substrate morphology, thus the organisms can “engineer” an impact on the hydraulics beyond that of their own physical bodies [4]. Because of the complex shape and structure of organisms and ecosystems, and complicating factors such as the flexibility of plants, parameterizing the influence of benthic ecosystems on hydraulics has been a difficult (and, as yet, largely unsolved) problem that has attracted much research in recent decades [22].

The role of ecosystem spatial heterogeneity in determining ecohydraulic interactions and their ecological, hydraulic, sedimentary, morphological and biogeochemical implications is a topic that has only recently received attention, but a rapidly growing body of literature is emerging in this area. This paper combines results from a number of studies to develop a synthesized picture of the understanding that has been developed in this area from the laboratory flume modelling they report, and to identify potential future research directions. The experiments have used either real or simulated versions of two keystone organisms in coastal waters: seagrass, in particular the Mediterranean seagrass *Posidonia oceanica* (Neptune grass), and blue mussels (*Mytilus edulis*).

Seagrasses have been studied extensively for several decades, and are hugely important along coastlines worldwide for many reasons. They provide sediment anchoring and protect coasts by damping waves and storm surges; they sequester carbon highly effectively; they provide important nursery and sanctuary habitats for a

wide range of species, as well as food for many others including “charismatic megafauna” such as dugongs and green turtles; they oxygenate water highly effectively and play a significant role in nutrient cycling [24].

Blue mussels are sessile, benthic, bivalve filter feeders that support diverse coastal ecosystems. Their main food source, pelagic algae, is supplied by hydrodynamic advection and turbulent diffusion [28]. Their major stressor, especially in soft substrate environments, is hydrodynamic forcing which can wash them away. Hence, their spatial distribution is predominantly a response to hydrodynamics. Hydrodynamics also determines the transport of particulates, which determines bed topography around mussel beds, and the dispersion of mussel larvae. These set conditions for the evolution of mussel beds, and the ecosystems that they support, at landscape scale.

2 METHODS

A number of different flumes were used in these experiments. They all had widths of between 0.5 and 1.0 m, and held water up to depths of 0.4 m. They had long sections of upstream flow, and various forms of damping and collimation at the upstream end, so that secondary flows were minimized by the time the flow reached the experimental section. Patches of the organisms or organism simulants were prepared on boards that filled the width of the flume, and since the flow fields that were passed over them were also essentially uniform across-flume, the experiments were essentially two-dimensional. The seagrass simulants were created from strips of polyethylene, which matched the geometric and mechanical properties of natural plants. The mussel experiments used either shells from dead mussels (in a freshwater flume) or live mussels (in a seawater flume).

The experiments proceeded by passing flows over the organisms at speeds representative of natural flows, ranging from a few to several tens of cm s^{-1} . All of these flows were strongly sub-critical ($Fr < 1$) and turbulent ($Re > 5000$). Velocity measurements were made with Acoustic Doppler Velocimeters (ADV), at points at several different heights within profiles located at downstream positions. From these, the state of the flow upstream, over (or within), and downstream of the organisms could be determined. Components of mean flow speed in the along-flume (u), across-flume (v) and vertical (w) directions were calculated from the time series of three-dimensional ADV measurements $\{U(t), V(t), W(t)\}$ recorded at each measurement point. These mean speeds were then subtracted from the corresponding initial time series to give time series of fluctuating velocity components $U'(t)$, $V'(t)$ and $W'(t)$ (i.e. $U'(t) = U(t) - u$ etc.). Turbulent flow components u' , v' and w' were calculated as the root mean square values of these fluctuating component time series. From these, various turbulence parameters could be calculated, the most commonly used of which was the turbulent kinetic energy per unit mass of water (TKE), which was calculated at each measurement point as

$$\text{TKE} = \frac{1}{2} (u'^2 + v'^2 + w'^2) \quad (1)$$

These measures of the mean and turbulent components of the flow were then analysed to derive understanding of the interactions between the flow and the organisms or simulants.

3 RESULTS

3.1 Seagrass experiments

3.1.1 Patch-wake-patch interactions

Folkard [6] studied the structure of the flow and turbulence fields in the vicinity of pairs of seagrass patches. Given the two-dimensional nature of the configuration, on reaching the first patch, the flow was largely forced over the top of it, creating the well-known mixing layer at the top of the canopy [13] between the rapid overflow and the slower flow through the canopy. When this layer separated from the patch's downstream end, it formed a wake, in which “near-wake” and “far-wake” regions could be identified (Figure 1).

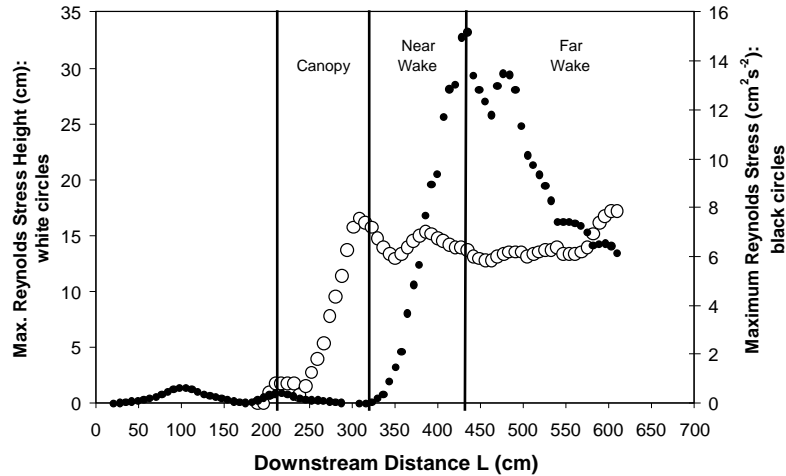


Figure 1: Illustration of near-wake and far-wake phenomenon

In the near-wake, the mean flow shear remained strong enough that turbulent creation was greater than turbulent decay, and the Reynolds stress increased in magnitude. In the far-wake, turbulent decay dominated, and the Reynolds stress decreased. The effect of the upstream patch on the flow conditions experienced by the downstream patch was found to depend on the relative positions of the upstream edge of the downstream patch and the turbulence maximum in the upstream patch's wake (see Folkard [6] for details). Thus the ratio of patch separation (an ecosystem trait) to the length of the upstream patch's near-wake (a trait of the hydrodynamics) is key to quantifying the "hydro-climate" within the downstream patch. This hydro-climate is likely to be important in governing ecological and sedimentary processes within the downstream patch.

3.1.2 Flow structure in gaps

Subsequent work focused on gaps in seagrass meadows – the inverse of isolated seagrass patches. The flow field over this type of configuration was studied by Maltese et al. [19], who focused on quadrant analysis and found that the flow above the canopy was dominated by sweep and ejection events. These structures continued over the gap, implying that coherent vortices formed over the meadow by the Kelvin-Helmholtz instability [14] were advected, and grew in the wake across the gap. As the flow adjusted to the gap, the centre of the wake dropped towards the flume bed, but rose again at the onset of the meadow downstream of the gap. Beneath this, the overhanging leaves from the upstream canopy created a near-stagnant region at the upstream end of the gap, where flow conditions were similar to those inside the meadow. Downstream of this, a recirculation cell formed due to flow separation from the upstream canopy, after which the flow re-formed a boundary layer above the bed (Figure 2). Depending on the length of the gap, this pattern was interrupted at some point by the onset of the canopy at the downstream end of the gap [7].

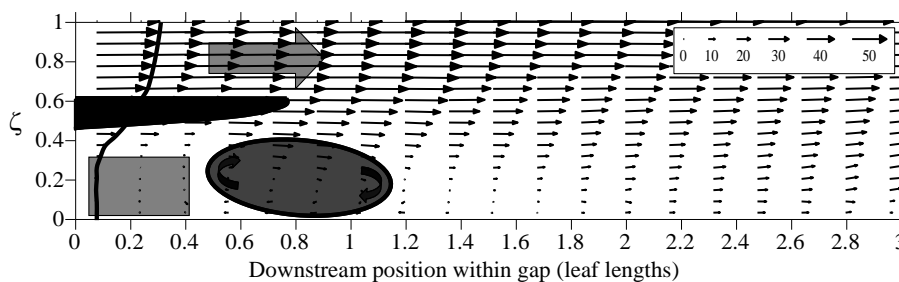


Figure 2: Sketch of flow structure within a gap in a simulated seagrass meadow, from [7]. The arrow-shaped shaded area indicates the strong overflow above the canopy; the rectangular shaded area indicates a region of essentially stagnant flow; the elliptical shaded area indicates a flow recirculation zone; the fourth, elongated shaded area indicates the overhanging plant canopy.

Thus, as above, the relationship between the size of the gap and the flow structures created by hydrodynamic interaction with the organisms' spatial configuration determined the conditions in the gap. Folkard [8] categorized these conditions into five types, extending the concepts of skimming flow, wake interference flow and isolated roughness flow coined by Morris [20]:

1. Skimming flow, in which the gap is too short to allow formation of a re-circulation cell, so only the near-stagnant region in Figure 2 is present, and most of the flow passes over the top of the gap.
2. Recirculation flow, in which the gap is long enough to allow a recirculation cell to form, enabling some ventilation of the gap, but is not long enough to allow formation of boundary layer flow.
3. Boundary layer recovery flow, in which the gap is long enough to enable a boundary layer to re-form, but short enough that the upstream canopy's effect is still felt by the canopy downstream of the gap.
4. Through-flow, in which the flow through the canopy is sufficiently strong, and the overflow sufficiently weak, that the latter does not form a recirculation cell, and the flow in the gap is dominated by flow coming through the upstream canopy, rather than over it. This can be thought of as a form of skimming flow, in that there is no momentum exchange between the flow within the gap and the overflow above.
5. Isolated roughness flow, in which the gap is long enough that a turbulent boundary layer in equilibrium with the bed is achieved before the downstream end of the gap, and thus the downstream canopy is not affected at all by the hydrodynamic alterations caused by the upstream canopy.

The occurrence of these regimes is dependent not only on the geometry of the patch (i.e. its length to depth ratio [8]), but also the plants' density and rigidity, and the flow speed. The flow within these gaps is qualitatively different from flow in gaps between impermeable obstacles (e.g. buildings, dunes), in that through-flow from the upstream canopy and the role of overhanging leaves can be important. Recent work [2] has further investigated the hydrodynamics of gaps in seagrass meadows. These experiments all fell into the throughflow category, but distinguished between cases where there was significant intrusion of overflow into the gap, and those where the overflow was effectively sealed off from the gap. A similar approach was used to investigate changes in the canopy throughflow in the downstream canopy (and therefore resource supply to this canopy) as the gap shape changed. A clear change in behavior was found around a gap height to length ratio of 0.3. When the ratio was <0.3 (i.e. for longer, lower gaps), there was both significant intrusion of the overflow into the gap, and significantly increased throughflow in the downstream canopy. Above this value, both of these were limited. The ratio value of 0.3 is the same as that reported by Oke (1988) as the value below which isolated roughness flow occurs in the context of urban buildings.

3.1.3 Meadows with varying, non-zero plant density

Adhitya et al. [1] investigated an intermediate form of heterogeneity, where meadows contain regions of low and high density seagrass. This investigated the four possible configurations of two patches of high density seagrass (1100 shoots m^{-2}) and two patches of low density seagrass (400 shoots m^{-2}), as illustrated in Figure 3.

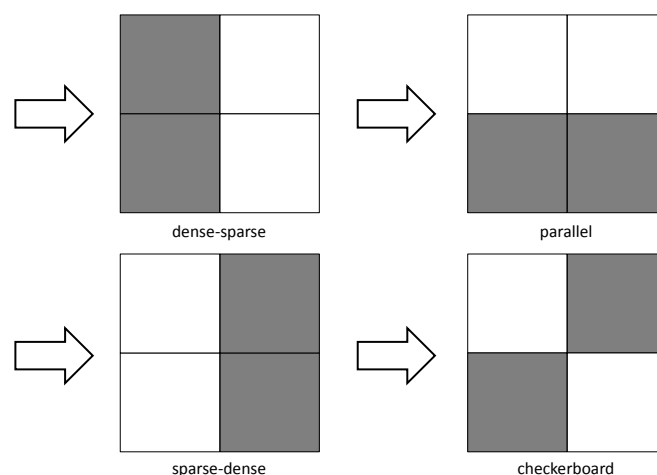


Figure 3. Sparse and dense patch configurations used by [1]. Darker squares are dense patches, lighter ones are sparse patches. Arrows indicate flow direction.

In all cases, the combined patches covered the full width of the flume. The results showed that, regardless of configuration, the volumetric flow rate was greater through the low density patches. If we take this flow rate as a proxy measure of resource supply to the seagrass, this implies that, in resource-limited contexts, the hydrodynamics favour growth in lower density patches, and thus encourage homogeneity in seagrass meadows.

3.2 Mussel experiments

3.2.1 Effects of gap edges

We measured the flow structure around a single mussel patch, and calculated the depth integrated turbulent kinetic energy as a measure of the level of turbulent mixing occurring at each downstream location (Figure 4).

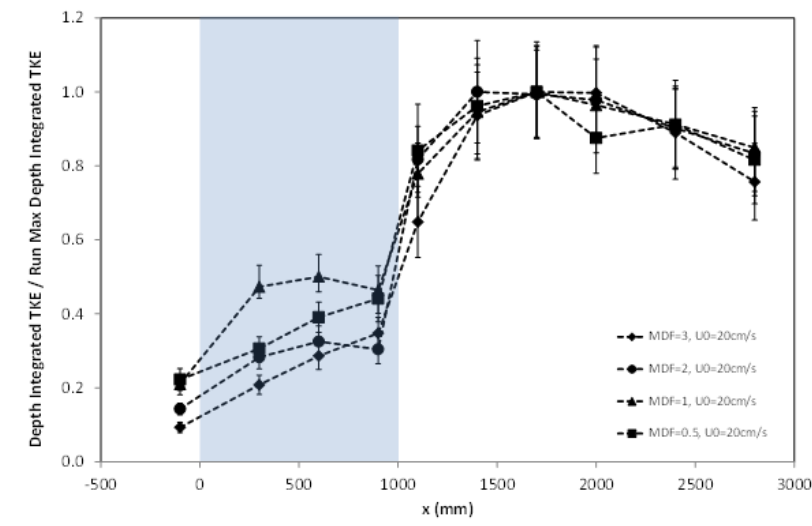


Figure 4: Change in turbulent kinetic energy (TKE) as flow passes over a mussel patch (shaded area). Symbols indicate values of mussel density (MDF) and mean flow speed (U0) (Folkard and Bouma, unpublished data)

Figure 4 demonstrates the importance of the patch edges, and in particular the downstream edge, for turbulence generation. This suggests that these edges are the most important element of mussel patches for generating turbulent energy which can mix food down to the mussels. This is needed to balance the consumption of food provided by horizontal advection at the front end of the patch, which can create “concentration boundary layers” around the mussels in which food concentration is strongly depleted [12].

To test this suggestion, we investigated the effects of varying the number of patch edges within a constant amount of mussel bed [11], using 2-patch and 4-patch configurations (Figure 5).

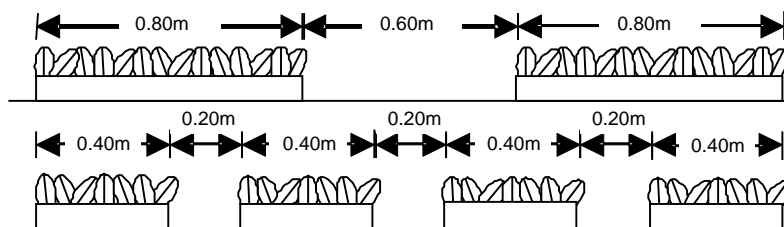


Figure 5: Configurations used to investigate effect of mussel patch edges on flow (Folkard and Gascoigne, 2009)

We found that the depth integrated TKE at the downstream end of the set of patches was ≈ 1.8 times larger in the 4-patch case than the 2-patch case. In the 4-patch case, $\approx 70\%$ of the TKE was in the bottom 5cm of the profile, compared with $\approx 55\%$ for the 2-patch case. This implies that in the 4-patch case, turbulence generation events near the bed occur more often, and there are fewer opportunities for the turbulence to diffuse vertically.

3.2.2 Effect of flow structure on mussels' stresses and facilitations

Subsequently [10], we considered the effects of variations in flow speed and the coverage density of a mussel patch on hydrodynamically-mediated stresses (bed shear stress) and facilitations (horizontal and vertical food supply) that determine mussel spatial distribution. We used three parameters as measures of these stresses and facilitations: the mean bed shear stress; the mean flow speed close to the bed (horizontal food supply), and the TKE in the overflow (vertical food supply). The results indicated that as mussel bed coverage increased up to 100%, the speed of horizontal advection over the patch decreased, the rate of vertical turbulent diffusion above the patch increased, and the bed shear stress on the patch didn't change significantly. Overall, therefore, there appear to be more benefits than stresses associated with mussels increasing their coverage up to 100%. When we increased the coverage over 100% (i.e. mussels piled on top of each other), there was no clear pattern of changes to benefits or stresses. Downstream of the patch, its wake is clearly beneficial to subsequent mussel patches: its turbulence causes replenishment of food at the mussels' elevation height, both from above and by re-suspending bed material. However, our experiments found no systematic relationship between patch coverage and the strength of these effects.

4 DISCUSSION

The configurations of our seagrass and mussel experiments are hydrodynamically-distinct from each other. Whereas the seagrass configuration has an elevated canopy which creates a mixing layer at its top, the mussel patches are essentially enhanced surface roughness, over which an adjusted boundary layer forms. The mussel patches do, however, have a small amount of elevation associated with them, though their impermeability does not allow a mixing layer structure to form over them. This fundamental difference in ecosystem morphology results in different consequences of their flow interactions.

There are, however, also many similarities between their interactions with flow. Perhaps the most significant is the importance of edges, in particular downstream edges. In the seagrass experiments, the downstream patch edge was the site of flow separation and formation of the structures that determine the hydro-climate within the subsequent gap and the seagrass meadow downstream of the gap. In the case of the mussels, the downstream patch edge was the site of maximum turbulence generation that can supply food to mussels downstream. An increased density of patch edges was found to cause increased turbulence, implying that this may be an important factor causing the complex (and thus multi-edged) patterning seen in many mussel beds [18].

The flow structure in gaps downstream of a seagrass patch is clearly determined by the spatial relationship between the patch's wake and the length of the gap. Where the gap is short, and skimming flow occurs, one would expect Nepf and Vivoni's [21] division of vegetation canopies into horizontal exchange zones (within canopies) beneath vertical exchange zones (near the tops of canopies) to characterize the gap as well. In this case, the wake acts as a lid on the gap, and life within the gap will be similar to that within the meadow, at least in terms of the hydro-climate, and therefore particulate and solute fluxes. Where the gap is longer, there is space for more flow development, and the diversity of flow conditions (near stagnation, recirculation cell, boundary layer) suggests that there will be a similar diversity of sediment characteristics and habitats. Canopy edges are known to be contributors to habitat diversity [3]; the work presented here elucidates how the hydrodynamics contributes to this. In these longer gaps, particulate deposition will be more important. This will alter landscape-scale budgets of particulates including mineral sediments, pollen, seeds, and pelagic larvae [15]. Often, gaps are spaces for competition between pioneer vegetation and existing vegetation, in which faster growing species can colonize gaps in meadows of other species [25]. To do this, their seeds must be delivered from outside of the meadow, most likely by flow over the meadow. Our results imply that this process is more likely to happen in longer gaps, and that "skimming flow gaps" are more likely to be filled by rhizome extension from plants at the gap's edge.

In mussel beds, flow structure in gaps is likely to be less varied, because of the less detailed flow structure. In our experiments, we found no flow separation and no stagnation zone. Instead, flow in gaps between mussel patches was characterized by a sharp increase in turbulent energy, implying a strong exchange of solute and particulates between the near-bed region and the overlying water column. On a large scale, more gaps and more patch edges would tend to increase both hydraulic roughness and fluxes between the bed and water column.

Results from both the seagrass and mussel experiments indicate the influence of hydrodynamic adjustments caused by one patch of organisms on subsequent patches downstream. As for gaps, the nature of these influences depends on the spatial relationship between the flow structures and the patch spacing, a fundamental eco-hydrodynamic interaction. This is important for seagrass patches where the hydro-climate within the downstream patch is determined by its position relative to the turbulence maximum of the upstream patch's wake. It is also important where regions of low and high density seagrass are found adjacent to each other. Here, our results suggest that the hydrodynamic processes encourage meadow homogeneity. In mussel beds, the patch spacing determines the extent to which food sources can be replenished for downstream patches after being denuded by the feeding of upstream patches.

Overall, this work has identified several implications of eco-hydraulic interactions in fragmented distributions of seagrass and mussels. At patch scale, it has shown them to be dominant determinants of the hydro-climate and of particulate and solute fluxes within gaps and patches downstream of gaps. At landscape scale, it suggests the importance of the density of patch edges in determining the macro-scale hydraulic roughness of these ecosystems, and the food supply to mussel beds. It also suggests that the size of gaps in seagrass meadows is important in determining landscape-scale particulate budgets, and the extent to which rapidly colonizing pioneer species can infiltrate established beds of other species, and that the hydrodynamics of seagrass meadows of varying density tend to move them towards homogeneity.

5 CONCLUSIONS

The results presented show that the type of laboratory flume experiments discussed here can be beneficial in providing insights into eco-hydraulic interactions in heterogeneous ecosystems, and illustrate the importance of hydraulic understanding for predicting the ecological implications of these interactions. Several approaches can be taken to building on these studies, all of which imply a need for a loosening of the reductionist tendency to idealize and simplify. Firstly, the configurations used could be made more realistic. For example, given the importance of patch edges, a move could be made away from sharp-edged configurations. Although organism patches in nature can be sharp-edged, often their edges are less distinct. Thus, it would be beneficial to study the hydrodynamics of gradual gradients in organism density, and this might also elucidate how patch boundaries evolve and are governed, and thus what controls patches' growth. Secondly, there is a need to incorporate 3D structures into flume models. The 2D structure of flumes discourages this, but researchers have started to explore 3D structures in laboratory flumes [30], and there is scope for much more work in this area. Thirdly, attempts to bridge the gap between laboratory and field studies would be beneficial, bringing more natural conditions into flumes or more control to field-based studies. This has been tried by, for example, using real organisms in laboratory flumes [29], or field flumes. An alternative approach [9] is to use simplified obstacles (e.g. sandbags or wooden stakes) in otherwise natural channels. Finally, the value of hydraulicians, ecologists and scientists from other fields working together cannot be overstated: the combination of their varied approaches to the understanding of biophysical interactions and their implications has the potential to be very powerful.

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