

## State of Science

# Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology

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**ABSTRACT:** There appears to be no single axis of causality between life and its landscape, but rather, each exerts a simultaneous influence on the other over a wide range of temporal and spatial scales. These influences occur through feedbacks of differing strength and importance with co-evolution representing the tightest coupling between biological and geomorphological systems. The ongoing failure to incorporate these dynamic bio-physical interactions with human activity in landscape studies limits our ability to predict the response of landscapes to human disturbance and climate change. This limitation is a direct result of the poor communication between the ecological and geomorphological communities and consequent paucity of interdisciplinary research. Recognition of this failure led to the organization of the Meeting of Young Researchers in Earth Science (MYRES) III, titled 'Dynamic Interactions of Life and its Landscape'. This paper synthesizes and expands upon key issues and findings from that meeting, to help chart a course for future collaboration among Earth surface scientists and ecologists: it represents the consensus view of a competitively selected group of 77 early-career researchers. Two broad themes that serve to focus and motivate future research are identified: (1) co-evolution of landforms and biological communities; and (2) humans as modifiers of the landscape (through direct and indirect actions). Also outlined are the state of the art in analytical, experimental and modelling techniques in ecological and geomorphological research, and novel new research avenues that combine these techniques are suggested. It is hoped that this paper will serve as an interdisciplinary reference for geomorphologists and ecologists looking to learn more about the other field. Copyright © 2010 John Wiley & Sons, Ltd.

## Introduction

The predominant view in many fields of natural science has long been that biology is an epiphenomenon of the physical environment. A cursory look at textbooks in biology, geology, chemistry, and others reveals the vast number of paradigms that are founded on the idea that the abundance, biomass, and distribution of organisms on the planet is dependent upon spatial and temporal variation in physical processes, which constrain where life can exist and how much life can exist. This view has been prominent for many decades despite an earlier recognition within the natural sciences that life and its landscape are intimately related through 'interactions between the organic and inorganic' (Darwin, 1881; Tansley, 1935). Although feedbacks were not forgotten entirely, they received much less attention during the 20th century than many alternative topics, perhaps because increasing specialization and disciplinary boundaries minimized interactions among biologists and physical scientists (Renschler *et al.*, 2007; Corenblit *et al.*, 2008). However, in

recent decades researchers have returned to early views about bio-physical interactions, and have begun to show in detail how organisms not only respond to their physical environment, but also directly modify and control their physical environment in ways that promote their own persistence. Entire bodies of research such as biogeomorphology (Viles, 1988), 'ecological stoichiometry' (Sterner and Elser, 2002), 'ecosystem engineering' (Jones *et al.*, 1994), and 'biodiversity and ecosystem functioning' (Loreau *et al.*, 2002) have emerged to illustrate how the numbers and types of plants and animals that inhabit an ecosystem can directly control the fluxes of energy and matter that underlie biogeochemical cycles, gas fluxes, sediment transport, and the formation of new physical habitat. Complimentary developments in the field of 'ecohydrology' have also revealed numerous ways in which plants and animals can alter water flow paths and soil moisture/depth to the advantage of those species (McCarthy *et al.*, 1998; Rodriguez-Iturbe and Porporato, 2004; Yoo *et al.*, 2005b; D'Odorico and Porporato, 2006; Tamea, 2007; Muneepreakul *et al.*, 2008a, 2008b)

If physical processes drive ecosystem structure, while the evolving structure also modulates physical processes, then feedbacks between the two are likely to be important. However, not all bio-physical interactions will have a significant effect upon landscape functioning and an extreme end-member exists where life is absent from a landscape; deciding whether and where bio-physical feedbacks are important is a key challenge. Abiotic landscapes must have existed on Earth prior to the colonization of land by plants during the Silurian and they are currently observed on Mars (Dietrich and Perron, 2006; Corenblit and Steiger, 2009). The Earth's terrestrial landscape has undergone considerable modification since the Silurian in conjunction with the evolution of terrestrial life; the degree to which physical landscapes may co-evolve with biological systems is discussed in detail in this paper.

It has proven difficult to incorporate bio-physical feedbacks into existing (numerical, physical and conceptual) models in part because their importance depends upon the temporal (and likely spatial) scale under consideration (Schumm and Lichty, 1965), and more importantly because such feedbacks are likely to give rise to emergent behaviour that prevents the use of simple 'linearly additive' models (Werner, 2003). Yet the need to make society-relevant predictions has never been more important. Climate models are now entering an era where regional projections for temperature and rainfall changes are possible (IPCC, 2007). Unfortunately, our models for landscape evolution are not yet at this stage. What we need is to develop a new set of conceptual as well as mathematical models of life-landscape coupling that can account for emergent behaviour; fundamental science must be done to elucidate bio-physical coupling across a range of scales. To advance this goal and to promote interdisciplinary research efforts by ecologists and geomorphologists a group of early career scientists from around the world met at the third Meeting of Young Researchers in Earth Science (MYRES III) at Tulane University in 2008: discussion revolved around the theme 'Dynamic Interactions of Life and its Landscape'. During the course of 4 days of discussion, 77 competitively-selected international delegates explored several key areas for future research: can one demonstrate a definite signature of life in landscape form? how does the functional diversity of organisms influence and feed back on landscape change? and do the structures of landscapes and ecosystems co-evolve? In the following sections we expand upon these themes by identifying: (a) the state of the art; (b) knowledge gaps; and (c) ways forward in the study of bio-physical interactions. We also suggest two areas in which advancements in basic science will have immediate and important practical consequence: advancing the application and success of landscape restoration techniques, and predicting landscape susceptibility to destabilization from climate change.

During the MYRES workshop we also discussed some of the analytical, experimental and modelling techniques that are now available to ecologists and geomorphologists. It was surprising how little each of us knew of techniques and methods in other disciplines. In order that we may encourage interdisciplinary research, and to some degree explain what is possible, we begin this paper by outlining some of the most powerful analytical, experimental and modelling techniques in ecological and geomorphological research, and suggest novel research avenues that may combine these approaches.

## New Techniques and Methods

Recent decades have seen the development of a wealth of new techniques and technologies in both ecology and geomor-

phology. There are enormous benefits to be gained in integrating these 'tools' to answer some of society's most pressing issues. We present here an overview of some of the most powerful and/or most underutilized techniques of which we are aware. Numerical and physical modelling are discussed in separate sub-sections due to the scope and complexity of these topics. We hope that this overview and attendant bibliography will serve as a useful starting point for future interdisciplinary research.

## Analytical tools for the field and laboratory

### State of art

Perhaps the most pervasive and most underutilized 'toolbox' currently available to ecologists and geomorphologists is that of remote sensing. Remote sensing is a term which encompasses both the science behind image acquisition hardware and the subsequent processing of data supplied by those systems. A broad suite of systems and techniques are available, including:

- ground-based, close range proximal sensing instruments such as hyperspectral spectroradiometers (Milton *et al.*, in press) and high definition laser scanners (Wehr, 2008);
- airborne multispectral scanners, multispectral video systems, thermal imaging sensors, aerial photography, light detection and ranging (LiDAR) sensors (Lefsky *et al.*, 2002), and side-looking airborne RADAR;
- spaceborne satellite systems, including nadir-viewing multispectral sensors, interferometric synthetic aperture RADAR (InSAR) systems, and multiple view angle systems capable of capturing anisotropic signatures (Diner *et al.*, 1998).

The repeat survey capabilities of new multi- and hyperspectral remotely sensed systems and missions can now be employed towards the assessment of landscape change over a range of spatial and temporal scales. The Landsat series of satellites (Landsat 1 launched in 1972) can now provide up to 36 years of repeat-visit multi-spectral global coverage (Goward *et al.*, 2001; Williams *et al.*, 2006; Gillanders *et al.*, 2008) and this long time series has benefited studies of vegetation change and ecological modelling (Cohen and Goward, 2004). Further developments in the Landsat mission are planned with the Landsat Data Continuity Mission (LDCM), due for launch in 2012 (Irons and Masek, 2006; Wulder *et al.*, 2008). Active systems such as RADAR and LiDAR produce their own electromagnetic radiation, offering near-all-weather capabilities. These systems are primarily used for monitoring structure – either of the land surface or of the overlying vegetation (Rabus *et al.*, 2003; Parker *et al.*, 2004; Watt and Donoghue, 2005; Su and Bork, 2007; Moorthy *et al.*, 2008; Straatsma *et al.*, 2008).

More recently, the NASA Earth Observing System (EOS) has provided repeat-visit products from which physical landscape properties and dynamics may be obtained (Katra and Lancaster, 2008; Rowan and Mars, 2003). New opportunities for fine-scale observations are now possible, from a new generation of satellite sensors such as IKONOS (Hurt *et al.*, 2003), Quickbird (Clark *et al.*, 2004; Wang *et al.*, 2004) and SPOT-5 (Pasqualini *et al.*, 2005) which have multispectral pixel resolutions of 10 m or less. On the ground, field-based spectroradiometers offer even finer spectral and spatial resolution data (Anderson and Kuhn, 2008). When combined with local and regional observations of water and sediment yields, such observations can be used to relate bio-physical process interactions over a wide range of temporal and spatial

scales (Hilker *et al.*, 2008; Chen *et al.*, 2009; Connolly *et al.*, 2009).

Alongside the development of remote sensing techniques has been a concomitant revolution in field and laboratory techniques. A suite of stable and radioactive isotopes now allow dating of sediment and bedrock ages (and erosion rates) over a wide range of temporal scales. Short lived isotopes such as  $^{210}\text{Pb}$ ,  $^{241}\text{Am}$  and  $^{137}\text{Cs}$  enable dating of buried sediment over the past ~150 years (Appleby and Oldfield, 1978, 1992; He and Walling, 1996), with new high-resolution techniques allowing the near-annual dating of deposits from individual floods (Aalto *et al.*, 2003; 2008), plus independent determination of surface exposure time for sediments on floodplain surfaces. New advances also allow the measurement of extremely low  $^{14}\text{C}$  concentrations, enabling the dating of organic material up to 60 kyrs old (Bird *et al.*, 1999; Turney *et al.*, 2001, 2006). Radioactive cosmogenic nuclides ( $^{10}\text{Be}$  and  $^{26}\text{Al}$ ,  $^{36}\text{Cl}$ ) can determine the age of sedimentary deposits up to 5 Myrs old (Granger and Muzikar, 2001), while stable nuclides such as  $^3\text{He}$  and  $^{21}\text{Ne}$  can be used to date multi-million year old bedrock surfaces (Schafer *et al.*, 1999). Optically stimulated luminescence provides an independent (non-radiometric) technique for measuring the age of buried sediment over the same age range as  $^{14}\text{C}$ , and in rare instances  $>10^5$  years (Huntley *et al.*, 1985; Jain *et al.*, 2004). Another extraordinary technique allows us to estimate the upstream erosion rate of an entire river catchment from a single river sediment sample:  $^{10}\text{Be}$  concentrations in river-borne quartz integrate erosion rates over  $>10^2$  years (Brown *et al.*, 1995; Bierman and Steig, 1996; Granger *et al.*, 1996). These new techniques have allowed us to quantify transience and persistence in erosional and depositional records in all terrestrial environments. For instance, it has been shown that the Antarctic dry valleys have remained essentially unchanged for several million years, due most likely to the almost complete absence of water – and, by extension, ‘life’ (Summerfield *et al.*, 1999). Conversely, extremely rapid rates of erosion and sediment compaction ( $<26\text{ mm year}^{-1}$ ) have been measured in high mountains and deltaic environments, respectively (Schaller *et al.*, 2005; Reinhardt *et al.*, 2007; Tornqvist *et al.*, 2008). Rates of human disturbance of physical processes have also been quantified, e.g.  $^{137}\text{Cs}$  carbon inventory measurements (Van Oost *et al.*, 2007).

#### Knowledge gaps

There appears to be enormous untapped potential in the vast amounts of data currently available to researchers. Remote sensing tools, particularly satellite based systems, generate data at a pace that outstrips the average user’s ability to utilize it fully. These ‘tools’ offer adequate spatial resolution of the Earth’s surface but observing bio-physical interactions typically requires a higher temporal resolution than is currently available. We need to be able to observe feedbacks such as those between landslides and vegetation colonization in steep mountain terrain, and the response and recovery of landscapes to forest fire. In addition, we have few tools for measuring subsurface heterogeneities and biological activity and none of them provide the type of global cover that is now routinely available through remote sensing. This is a critical knowledge gap as a large proportion of ecological activity and biogeochemical cycling occurs in the subsurface; groundwater flow is also a key parameter in hydrological models.

A more general knowledge gap lies in the relatively short record of measured landscape dynamics ( $<10^2$  years). Many biological processes operate over decadal or shorter timescales (with peat development being an obvious exception) and

are therefore amenable to direct measurement. Unfortunately, physical processes operating over much longer time period are difficult or impossible to measure directly. Perhaps more importantly we have thus far been unable to quantify the timescale of bio-physical *interactions* in most situations: one of the classic examples is precipitation recycling through evapotranspiration, which could influence landform development over millennia (Worden *et al.*, 2007). In this context it is crucial that we use reliable palaeo-landscape proxies to quantify landscape dynamics.

#### Ways forward

Palaeo-community dynamics are now accessible through a variety of proxies (e.g. plant macrofossils (Birks and Birks, 2000), testate amoeba – bog water tables – (Charman, 2001), pollen (Heikki and Bennett, 2003), and stable isotopes (Melanie *et al.*, 2004)). Of particular note is recent work by the PollandCal group which may enable the spatial distribution of palaeo-plant communities to be reconstructed from fossil pollen (Gaillard *et al.*, 2008). Progress is also beginning to be made in integrating palaeo-ecology with landuse/land cover records (Dearing *et al.*, 2008). The pace of progress can be accelerated if the suite of cutting edge analytical technologies in both ecology and geomorphology are integrated. Remotely sensed imagery, numerous isotopic proxies, biomarkers and genetic analyses now allow determination of the physical and ecological structure of modern landscapes. To our knowledge, no study to date has combined the best of these approaches.

New isotopic proxies for physical and biological processes and new methods for analyzing high-resolution data sets are emerging all the time. Biological organisms fractionate isotopes such as carbon, oxygen and sulfur, while physical processes may fractionate calcium and strontium (for example), providing a parallel set of stable isotopes. Combining such proxies would allow unprecedented reconstructions of the chemical conditions of the past. If coupled with traditional stratigraphic analysis, plus modern analogue studies of where and how isotopes are fractionated, biogeochemical methods would allow us to extend the record of bio-physical interactions into deep geologic time.

Aside from the technical advances in the use of isotopes and remote sensing there are many new statistical methods that may help integrate ecology and geomorphology. We argue in this paper that there is no single axis of causality between life and its landscape, but rather, that each exerts a simultaneous influence on the other. This perspective requires that we move away from univariate models of causality that assume a single independent and dependent variable, and move towards models that assume two or more processes are operating simultaneously – in other words, we must have methods to evaluate more complex, multivariate relationships where estimates must be made for numerous pathways at once. This is where statistical tools such as structural equations modelling (SEM) (Shipley, 2000; Grace, 2006), Bayesian hierarchical modelling (Gelman and Hill, 2007) and related methodologies are opening up new opportunities (Clark, 2007). These methods allow for the direct testing of hypotheses that are conditioned on more than one causal pathway. For example, SEM fits data from an observed covariance matrix among variables to a matrix that would be expected based on the hypothetical set of relationships among the causal and response variables. As such, these models allow one to test for simultaneous causality among two or more variables, to estimate indirect effects among variables, and to directly incorporate spatial or temporal feedbacks into a hypothesis.

## Development and validation of landscape evolution models that enable feedbacks between biological and physical processes

### State of the art

To date, biological effects have been incorporated into four general types of geomorphic transport law (GTL) used to model: transport rates, thresholds of motion, slope stability, and hydraulic roughness (*cf* Dietrich *et al.*, 2003). In most of these numerical formulations biotic effects implicitly control the value of a parameter, such as thresholds for slope stability and fluvial incision, rather than acting as an explicit dynamic variable that interacts with geomorphic processes (see review by Dietrich and Perron, 2006). Initial steps in advancing GTLs for bio-physical interactions have included the development of equations that explicitly incorporate the dynamics of animal population (Yoo *et al.*, 2005b) and root density to soil depth (Roering, 2008). Other recent developments include GTLs that relate landslide initiation to forest growth and death (Benda and Dunne, 1997; Lancaster *et al.*, 2003), or human-induced land use change (Vanacker *et al.*, 2003b) and solve simple dynamic equations describing vegetation-erosion interactions over storm and inter-storm timescales forced by random rain events (Figure 1) (Tucker and Bras, 1999; Collins *et al.*, 2004; Istanbuluoglu and Bras, 2005). Climatic and ecohydrological controls however have not been fully incorporated in these models (for simulations of large-scale basins) over geomorphically significant times-

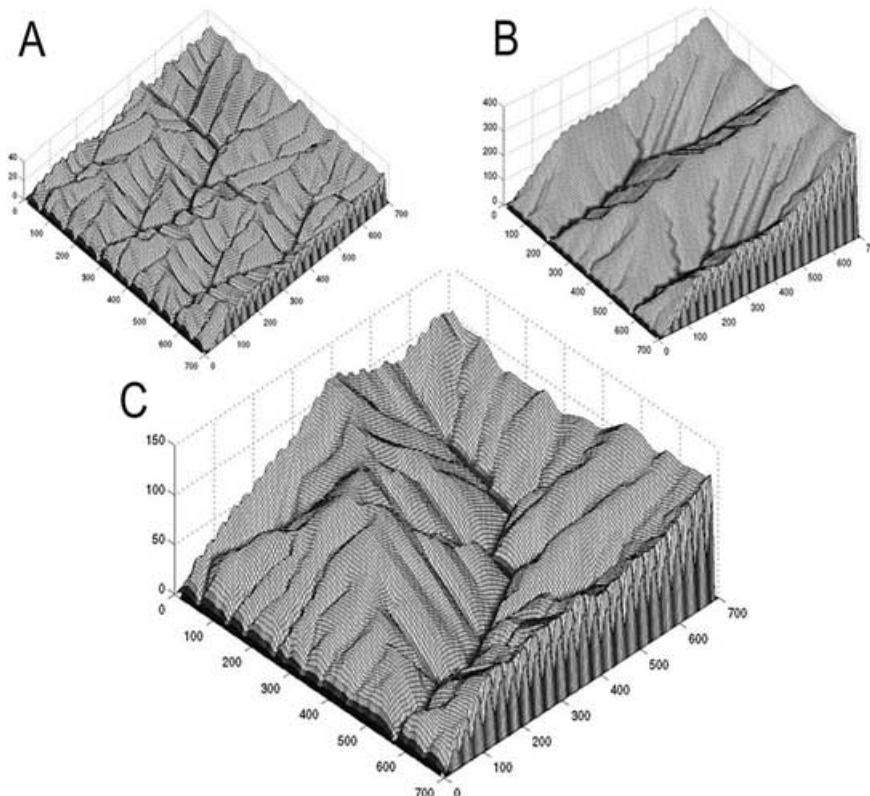
cales. Some recent analytical models of ecohydrological soil moisture, water balance, and vegetation dynamics that share the same simplistic view/spirit with the existing GTLs offer tremendous opportunities in this context (Rodriguez-Iturbe and Porporato, 2004). In the simplest sense, these interactions may be distilled into time-space integrated variables for long-term and large-scale landscape evolution modelling such as in the forms postulated below:

$$Q_s = KA^m S^n \quad (1)$$

and

$$K = \int_A f\{p, \lambda, B(t), k(B(t)), \tau_c(B)\} dt \quad (2)$$

where  $K$  is an integrated sediment transport coefficient,  $A$  is upslope contributing area,  $S$  is local landscape slope, and  $m$  and  $n$  are exponents that characterize the form of geomorphic transport (e.g.  $m = 0$  for creep and  $m > 1$  for wash). Equation (1) determines the transport rate ( $Q_s$ ) of sediment at any point on the landscape as a function of local topography and flow conditions (Howard and Kerby, 1983; Tucker and Whipple, 2002). In Equation (2),  $K$  is postulated to be an integrated coefficient that takes into account biomass as a dynamic state variable. In  $K$ ,  $p$  is mean storm intensity;  $\lambda$  is storm arrival rate;  $B$  is vegetation biomass;  $\tau_c$  is erosion threshold as a function of vegetation biomass,  $k$  is transport coefficient or erodibility that depends on both substrate size and plant biomass, and  $t$



**Figure 1.** Numerical simulations illustrating the contrasting difference in landscape morphology under conditions of constant uniform uplift and (A) no vegetation cover, (B) static uniform vegetation cover, (C) dynamic vegetation. All landscapes are in dynamic equilibrium, with mean elevations subject to fluctuations about a long-term mean. In the absence of vegetation (A) rainstorms generate frequent erosion events forming a highly dissected, low-relief topography. In the contrasting case (B), static (undying) vegetation protects the soil surface from runoff erosion. Continuing uplift under this condition increases the elevations until slopes exceed the critical threshold for landsliding and hillslope erosion is predominantly by mass wasting. In the third case (C) of dynamic vegetation, disturbances are driven by runoff erosion and landslides. Compared with the static vegetation simulation the outcome of vegetation-erosion coupling is a more highly dissected topography, with smaller landslide-dominated hollows entering the channel network; mean elevation is approximately three times smaller than that of the static vegetation simulation. The effect of wildfires on landscape development is explored in other simulations presented in this work (Istanbuluoglu and Bras, 2005).

is time. A numerical example of this model was given by Istanbuluoglu and Bras (2006), who used a bucket model of hydrology to examine the influence of climate fluctuations/change on potential sediment transport capacity. While such forms may be adequate for characterizing long-term and reach-scale average transport and incision rates, they may not capture sudden impacts of climate change and two-way interactions of vegetation and erosion.

#### Knowledge gaps

Subsuming biotic effects within existing GTLs is probably adequate in certain, as yet undefined, situations but our view is that in general more dynamic transport laws need to be incorporated into models. Plant biomass (both above and below ground), and some measures to quantify vegetation cover density, seasonality and the morphological diversity of plant structures (for example, differences in rooting structure), are necessary ecological variables for modelling the influence of vegetation on erosion and sediment transport. A recent paper by Montaldo *et al.* (2005) discusses vegetation models with various complexities that involve some of the aforementioned vegetation variables, and develops ways to simplify models as needed. In addition, numerical and physical modelling suggest that the destructive impact of erosion and/or deposition on an ecosystem (or disturbance as used in ecology literature) is just as important as the impact of vegetation on sediment transport mechanisms (see review by Murray *et al.*, 2008). Quantitative research into the impact of physical processes upon ecosystems has largely been confined to the ecological literature, although geomorphologists have begun to develop functional forms that relate vegetation loss to erosion and/or deposition and sediment transport for use in numerical models (Gyssels *et al.*, 2005). Most functional relations developed to date are lab based and upscaling to the landscape scale is problematic. In the existing literature the disruptive effect of erosion to the ecosystem is accomplished by rule-based approximations (Istanbuluoglu and Bras, 2005; Baas and Nield, 2007).

Determining appropriate temporal and spatial scales is usually a challenge in numerical modelling. Erosion rates and landscape patterns are known to exhibit a dependence on grid resolution in landscape evolution models (Passalacqua *et al.*, 2006). Choosing appropriate grid spacing requires some knowledge of the time and space scales associated with the processes we are trying to model. For example, in a model for river channel evolution, conservation of mass implies a 'morphodynamic' timescale while the numerical grid must be fine enough to resolve important features of the channel. Determination of the most relevant time and space scales for bio-physical interactions is critical to model success, as inappropriate selection may preclude feedbacks from arising. That requires, however, that these scales are *a priori* known, which is often not the case.

#### Ways forward

We view the development of verifiable predictive life-landscape models to be a key challenge. This new class of models needs to be simple enough to run over long-timescales, capture some of the most necessary aspects of climate-soil-vegetation-animal interactions, and have spatially explicit functions that allow competition between different vegetation functional types and species in space and time. The most relevant bio-physical processes responsible for shaping the landscape should be identified and included in the developing models. We stress the importance of nonlinear local interactions between animals, vegetation and physical processes through mechanisms such as grazing, seed dispersal,

and competition for soil moisture and light. Inclusion of these interactions will enable study of emergent patterns of landscapes.

1. There is momentum within the geomorphic modelling community towards integration of (or at least communication between) the wide variety of extant landscape evolution models. One of the most important initiatives in this regard is the Community Surface Dynamics Modelling System (CSDMS), which makes a host of numerical models available to the community ([www.csdms.colorado.edu](http://www.csdms.colorado.edu)). CSDMS has begun to encourage their modelling community to integrate formulations for dynamic bio-physical interactions within their hosted models (G. Tucker, pers commun.). Another promising type of model, which has successfully been employed in ecology in recent decades, is agent or actor based numerical modelling (Judson, 1994). Such models employ a number of decision making entities that generally execute autonomy, communication/interaction and decision making (Parker *et al.*, 2004), and appear capable of accommodating the complex interplay between humans and animals and their environment. This class of model is discussed in more detail later.
2. Developing new models that explicitly integrate biological and physical processes over the timescales of plant and human life or shorter is critical for modelling the human impact on the physical and the biological environment. Ecosystem dynamics operate at much shorter timescales than long-term GTLs, which are often calibrated over 1000-year timescales. The way forward is either to nest models requiring short timescales within longer-term surface process models, or alternatively, by examining separately the short-term transient dynamics of a system relative to the longer-term equilibrium dynamics (Hastings, 2004).
3. Determination of the timescales of physical and biological processes is key to understanding when, and how, they will interact. This also provides one potential path forward in dealing with issues of scale. For example, in considering whether vegetation dynamics interact with channel evolution in a river, one could determine both the characteristic timescale of vegetation growth and the characteristic 'morphodynamic' timescale of the river. In considering how the channel and vegetation interact, the absolute values of these two timescales are not important: rather, it is the ratio of these timescales that determines the nature of their interaction.
4. Statistical parameterization of smaller-scale processes may be required before we can generate large-scale mathematical models of heterogeneous systems. These techniques are already well established in the geophysics community: groundwater modellers use geostatistical methods to deal with permeability variations, and Large Eddy Simulation (LES) models parameterize the small-scale fluctuations of fluid turbulence in a statistical manner. Perhaps these statistical parameterizations can be used to model heterogeneity in rates of biological growth, chemical reactions and transport in large-scale landscape simulations. The LES approach has shown promise in resolving the grid-dependent issues of numerical landscape evolution models (Passalacqua *et al.*, 2006)
5. Simplified models for describing bio-physical feedbacks should be developed in parallel with more sophisticated landscape evolution models. While the ultimate goal of numerical modelling may be quantitative prediction, such predictive power is a long way off as many constitutive and dynamic relationships among variables have yet to be worked out (Fonstad, 2006; Phillips, 2006). Identifying

potential (nonlinear) feedbacks between physical and biological processes is necessary to make progress. In complex pattern-forming systems such as landscapes, the strong coupling among processes often dictates that system dynamics must be better represented than the details of individual processes (Murray, 2007; Murray *et al.*, 2008). Models that allow for a 'rules based' approach, like cellular automata (Fonstad, 2006), can serve to integrate mechanics and intuition in order to test ideas of life–landscape coupling. These models may be qualitatively and even semi-quantitatively predictive, but most importantly they can serve to generate hypotheses about the forms of physical and biological coupling in landscapes.

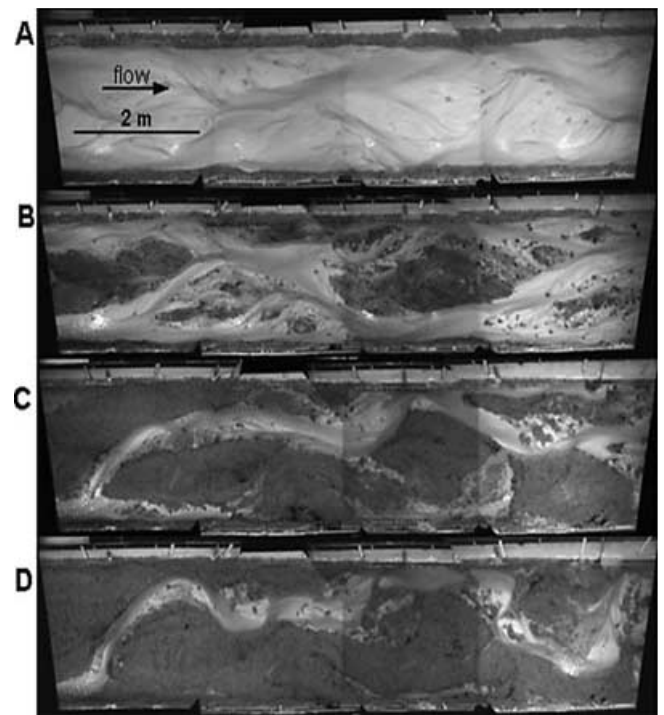
6. Model outputs must be compared in some way with independent data to be of scientific value. True verification of landscape evolution models is unlikely but validation in the sense that a model '*does not contain known or detectable flaws and is internally consistent*' is achievable (Oreskes *et al.*, 1994, p.642). Comparison of mathematical models with physical models may be beneficial in this regard as both methods are capable of *independently* producing the same result (i.e. a model landscape); direct comparison between independent models should also advance our understanding of bio-physical interactions. Current model tests are generally ambiguous and overly focused on weak topographic metrics. The modelling community needs to agree upon a suite of spatial and *temporally* sensitive tests of model output (Hoey *et al.*, 2003). These tests should allow for a hierarchal scale of model 'validations' of differing strength. Inclusion of ecological dynamics, which operate on relatively short timescales, may provide new temporally-sensitive tests.

### Physical modelling: motivating and constraining bio-physical experiments

#### State of the art

The use of experiments to physically model Earth surface processes has a long august history in geomorphology (Gilbert, 1914). Until recently the most effective experiments were prototype systems that were dynamically scaled down from field scales using dimensionless ratios. The strength of this approach is that if all relevant ratios are matched between experiment and prototype then measurements made in an experiment can be scaled up to the field (Paola *et al.*, 2009). However, models involving free flowing water (i.e. most surface process models) cannot be perfectly scaled to a laboratory size as no available fluid has a kinematic viscosity significantly less than water. Despite this limitation engineers have routinely shown that so long as the small-scale water flow is fully turbulent in both prototype and field then water can be used in prototype models (this is termed Reynolds-number independence in the literature).

It has recently been argued that formal scaling is unnecessary for a subset of landscapes that exhibit scale independence in their important processes. 'By scale independence we mean that the important dynamics of a system are independent of scale over a significant scale range' (Paola *et al.*, 2009, p.34). Scale independent systems would be unaffected by changes in scale and thus make natural targets for experimental study at reduced scale 'without recourse to classical dynamical scaling' (Paola *et al.*, 2009). If this new paradigm is correct it means that we can look forward to a rapid advance in our understanding of geomorphic systems within a sub-set of natural environments (Paola *et al.*, 2009): to-date this sub-set is thought to include high-relief mountains, braided channels



**Figure 2.** Results of a physical experiment designed to capture the interactions between vegetation, sediment, and water in natural rivers. The experiment begins with (A) a fully developed, self-formed, steady-state braided channel (sediment input equal to sediment output). A hydrograph was then introduced that oscillated between long-periods of low flow with no sediment transport, and high flows lasting 1 h that transported sediment and reworked channel morphology. Alfalfa seeds (*Medicago sativa*) were introduced and allowed to establish on emergent surfaces during each lowflow interval: vegetation increases bank stability and flow resistance and promotes deposition of cohesive fine sediment. The emergent landform is shown in (B) after six flood cycles, (C) after 18 flood cycles, and (D) after 23 flood cycles. By eliminating weak flow paths, the fast growing vegetation 'corrals' the water into a single dominant channel until the reduction in total wetted width leads to a new self-organized state in which the flow removes vegetated area as fast as it is produced. The new channel is deeper and has a broader distribution of depths than the braided one, with channel size adjusted to carry almost all the flood low (Tal and Paola, 2007).

and large depositional systems (Lague *et al.*, 2003; Kim and Paola, 2007).

The techniques and insights discussed above are largely focused on abiotic systems. However a new class of model has been developed that focuses on *single* species interactions with hydrogeomorphological systems. These models generally make some use of classical dynamical scaling but not all relevant ratios are formally scaled. Temporal scaling in particular is a problem when attempting to include a living growing plant in a prototype model. Nonetheless, these models are now producing exciting results that are amenable to field testing (Figure 2) (Gran and Paola, 2001; Coulthard, 2005; Tal and Paola, 2007).

#### Knowledge gaps

Rigorous scaling of physical models for purposes of landscape evolution is generally unfeasible except for the sub-set of geomorphic systems that exhibit natural scale independence in their important variables (Paola *et al.*, 2009). We have already discussed why true hydrodynamic scaling is often untenable and we add here that scaling sand sized and finer sediment is often difficult or impossible. Moreover, the need

for compressing time as well as space means that materials that erode or weather slowly in the field – like bedrock – cannot be scaled directly for laboratory experiments. In addition, rheologic and material properties of sediment mixtures may not be amenable to downscaling. A notorious example is the difficulty of creating meandering rivers in the laboratory, which is likely related to issues of downscaling sediment cohesion. For modelling bio-physical interactions, biota such as vegetation may well introduce fundamental length and timescales (related to the size and growth rate of plants, respectively) that cannot be reproduced in a laboratory. Conversely, some bio-physical interactions might include scale independence in their important variables as implied by some of the more successful experiments undertaken to date (e.g. Tal and Paola, 2007). This issue remains unresolved as we await the development of more robust theoretical basis for prototyping bio-physical interactions.

#### Ways forward

The use of classically dynamically scaled prototypes will continue to be an important investigative method. However, natural similarity seems to provide a far more flexible and expansive framework for experimental design and interpretation. It is not yet known how 'widespread natural scale independence is in morphodynamics, but the evidence to date suggests it is common' (Paola *et al.*, 2009, p.37). We will not know until researchers investigate this further, and comparison of bio-physical dynamics across scales is an obvious way to tackle this. Identifying the rates and timescales of important physical and biological processes, and how they compete to generate landforms is also of primary importance. We hypothesize that it is the relative – rather than absolute – timescales of competing processes that dictate pattern formation and evolution in simple bio-physical systems, and that correctly identifying and scaling them leads to dynamic similarity. For example, Jerolmack and Mohrig (2007) demonstrated that the relative magnitude of channel bank erosion and bed deposition timescales controls channel pattern, allowing direct comparison between field and laboratory observations.

It is unlikely that we will ever be able to dynamically scale ecological-community interactions in a small prototype. In a forthcoming section we discuss why ecosystem dynamics might be important to landscape functioning so here we confine ourselves to the practical issues involved in developing effective models. Modelling the interactions of many different species on an evolving landscape is not easy, because each organism introduced has its own length and timescales of growth. In addition, simplifying the experimental system requires neglecting variables. If very little is known about the nature of bio-physical feedbacks in a natural landscape, an oversimplified model may be constructed that precludes important feedbacks from developing. Field work has its own drawbacks, because the confounding effects of environmental variability make it difficult to separate cause and effect. Fortunately the development of field-scale experiments offers a way forward. There are now a small number of field-scale experiments that enable study of multi-species (ecological community) interactions with abiotic processes. One example is the 'Outdoor Stream Lab' at St. Anthony Falls Laboratory, Minnesota. This is a reach-scale system designed to study interactions among channel, floodplain and vegetation ([www.safl.umn.edu/facilities/OSL.html](http://www.safl.umn.edu/facilities/OSL.html)). Another example is at the University of Arizona's Biosphere 2, where several large experimental hillslopes are under construction (<http://www.b2science.org/Earth-hillslope.html>). This setup will allow the study of vegetation growth and its influence on hydrology, biogeochemical fluxes and sediment transport, through exten-

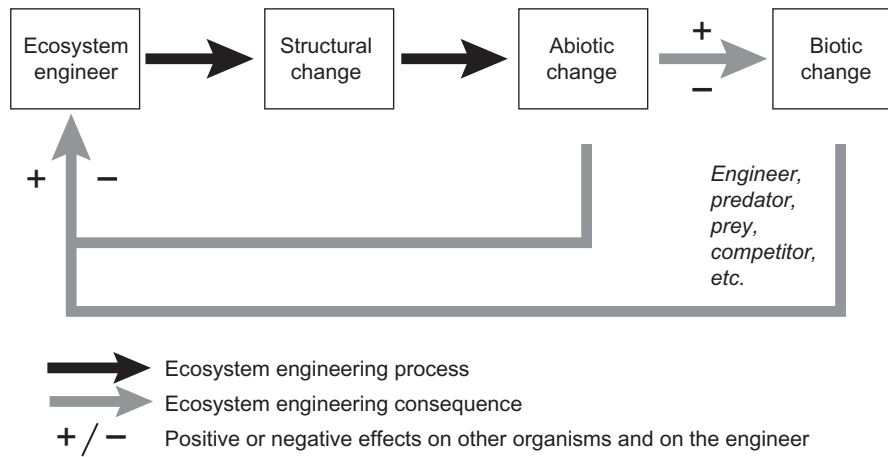
sive monitoring under carefully controlled conditions for approximately 10 years.

## Co-evolution of Landforms and Biological Communities

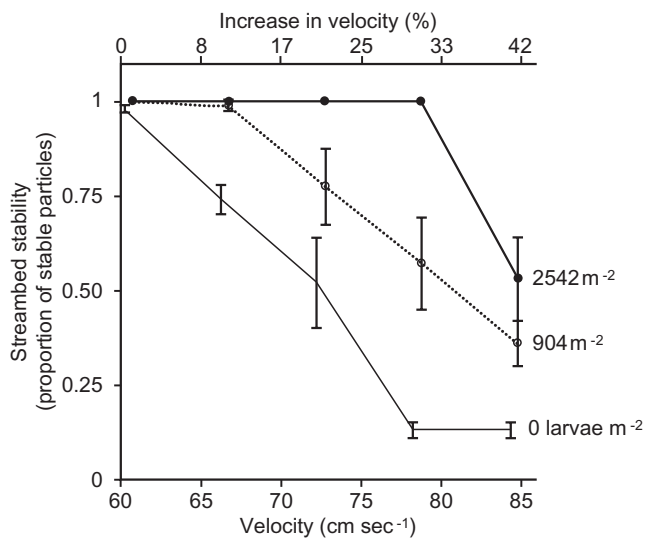
Within the field of biology, the term 'co-evolution' was coined to describe the simultaneous adaptation by populations interacting so closely that each exerts a strong selective force on the other (Ehrlich and Raven 1964). Co-evolution is a classic example of a feedback in which genetic, and subsequently, morphological change by one population induces change in a second population that, in turn, feeds back to stimulate further adaptation by the first. Although co-evolution is typically used to describe biological interactions and implies the action of natural selection, there are a number of conceptual parallels to bio-physical feedbacks whereby physical processes constrain the selective environment that drives biological evolution while the biotic community simultaneously modifies the physical environment at a variety of spatial and temporal scales (Urban and Daniels, 2006; Renschler *et al.*, 2007; Corenblit *et al.*, 2008). For purposes of this paper, we define such bio-physical forms of co-evolution as: '*feedbacks in which the physical environment regulates the numbers and types of organisms that can coexist in a community and shape the selective environment that drives evolution while, at the same time, the organisms themselves modify the environment in a way that enhances their own persistence.*' This definition does not imply that biological communities evolve as a group or whole. Indeed, the idea of community-level evolution (also called group selection) has been highly controversial; many argue there is no clear mechanism that can drive the evolution of groups that do not share common genes (Wilson, 1983). However, any collection of species or populations can share common life-history characteristics (growth rates, resource requirements, etc.) that cause them to respond to, or modify a landscape in a manner that is similar to one another. Furthermore, certain types of biological interactions like facilitation can cause the success of two populations to be mutually dependent. Thus, it is plausible for groups of organisms that comprise biological communities to simultaneously cause and respond to a changing landscape.

#### State of the art

There is a long and rich history of research in biology showing that changing landforms can cause changes in the abundance, biomass, numbers, and types of species that co-occur in any particular geographic location at a point in time. For example, the most widely cited mechanism to explain the formation of new life-forms is the process of allopatric speciation, which occurs when the formation of a geographic barrier (e.g. mountain range, canyon, or river) isolates two populations allowing them to genetically diverge from one another through time (Coyne and Orr, 2004). Paleobiologists and biogeographers have also shown that once species diverge, the distribution and survival probability of a new species is heavily influenced by geological processes, such as the movement of tectonic plates (Raven and Axelrod, 1974), volcanism (Miller, 1997), and the advance and retreat of glaciers (Hewitt, 1996). Even at smaller spatial scales, the field of ecology has shown that the assembly of ecological communities is strongly controlled by the frequency of disturbances (floods, hurricanes, landslides, etc.) that regenerate physical habitats and open up new niche opportunities that allow species to use untapped resources (Connell, 1979; Huston, 1979). Indeed, one could likely pick up any introductory textbook in these fields of



**Figure 3.** General pathways of physical ecosystem engineering (Gutierrez and Jones, 2008).



**Figure 4.** The field of 'ecosystem engineering' suggests that organisms directly create or modify habitat in ways that enhance their own persistence. As just one example, consider the results of Cardinale *et al.* (2004) who used a laboratory flume study to show that the construction of catchnets by net-spinning caddisfly larvae can increase the physical stability of substrates in streams. The more larvae (densities shown on right side), the more stable were substrates relative to control that had no organisms. Data points are the mean  $\pm$  SE from three replicate flumes.

biology and find dozens, if not hundreds, of examples where the organization of biological communities is presumed to be the outcome of physical processes that drive the formation of landscapes.

As discussed in the introduction to this paper the converse idea that biological communities act as an independent variable to drive the formation of landscapes is certainly not a new concept. For example, in his seminal book Vernadsky (1929) argued that life fundamentally shaped climate, atmosphere, and landforms. However, the role of biology in controlling rates of physical processes was not a prominent focus of ecological research until the 1990s when accelerating rates of species extinction forced researchers to pose the question . . . What do species do in ecosystems (Jones and Lawton, 1995)? One of the concepts to emerge during this period was that of ecosystem engineering (Figure 3), in which species tend to physically modify and/or create habitat in ways that can potentially enhance their own survival and/or the existence of other species (Figure 4).

Historical examples abound of organisms having large-scale effects on geomorphology and landscape formation. For example, Ives (1942) suggested that the valley floor elevation and 'false senility' of stream networks (i.e. extensive meanders and ox-bow lakes in relatively young stream networks) throughout the Rocky Mountains was due to the activity of beaver; subsequent research has supported this view (Naiman *et al.*, 1988; Gurnell, 1998). Mima mounds – Earth mounds approximately 20–30 m in diameter and as much as 2 m high, found throughout the western two-thirds of North America and other grassland habitats, have been hypothesized to have been created through soil translocation by fossorial rodents (Dalquest and Sheffer, 1942; Cox, 1984). Butler (1995) compiled an extensive list of examples of what he termed 'zoogeomorphology' or animals as geomorphic agents ranging from invertebrates to large mammals. The concept of organisms as ecosystem engineers has organized these scattered examples of organisms modifying the environment into a more general framework and has begun to make significant progress towards some unifying themes (Wright and Jones, 2006). Of particular importance are attempts to understand how variation in the spatial and temporal scale of ecosystem engineering affect the feedbacks to the ecosystem engineer and the consequences to the landscape (Gilad *et al.*, 2004; Jones *et al.*, 1997; Wright and Jones, 2006; Van Hulzen *et al.*, 2007). These examples of ecosystem engineering demonstrate that biological agents can alter the formation of landscapes. In many cases, the modification of landscapes by organisms would seem to be 'accidental', i.e. to offer little fitness advantage to the organisms themselves (what Odling-Smee *et al.*, (2003) called 'negative niche construction', or 'niche changing' sensu Dawkins (2004)). However, in other cases there are clear examples where modification of the landscape directly benefits the species. Such situations have been termed an 'extended phenotype' (Dawkins, 1999) or 'niche construction' (Laland *et al.*, 1999; Odling-Smee, 2003), and suggest that biology and landscape formation can feed back to simultaneously influence one another. Unfortunately, quantifying these types of feedbacks and showing they operate qualitatively in space or time lags far behind the speculation.

Perhaps the most advanced research in the area of co-evolution of landforms and biological communities stems from studies that have examined how biota both respond to and control sediment transport processes. Van Hulzen *et al.* (2007) described how *Spartina anglica* (common cordgrass) both modifies its habitat via its own physical structures, and then responds to those modifications. *Spartina* tends to enhance the accretion of sediments within the plant canopy



by reducing hydrodynamic energy and scour. Sediment accretion feeds back positively to enhance *Spartina* densities by increasing drainage and nutrient availability. But as sediment accretion leads to increased *Spartina* densities, gullies that form around the tussocks of plant growth inhibit the lateral expansion of *Spartina* through cloning of roots. In other words, the plant modifies the environment so that it becomes more locally favourable, but these modifications alter the process of erosion that create small 'islands' and inhibit spread of the plant. Other authors have shown how vegetation-driven sediment accretion enables vegetated surfaces to persist even under rates of sea level rise and sediment delivery that would normally preclude intertidal surfaces (and vegetation) from developing in the first place (Kirwan and Murray, 2007; Marani *et al.*, 2007). As a second example, it has long been known that the biomass, as well as composition and diversity of riparian plant communities along streams and rivers is controlled by flow regimes that influence the physical stability of bank habitats (reviewed in Naiman and Decamps 1997). However, recent laboratory experiments by Tal and Paola (2007) have shown that vegetation can also act as an independent variable to stabilize streambanks in ways that 'corral' the water and control the formation and stability of a channel. Thus, vegetation not only responds to channel formation and stability, it also directly influences it.

Modelling studies have also explored the two-way interplay between vegetation growth/succession and sediment transport in aeolian sand dunes (Baas and Nield, 2007), estuarine (Morris *et al.*, 2002; Mudd *et al.*, 2004; D'Alpaos *et al.*, 2007; Kirwan and Murray, 2007; Temmerman *et al.*, 2007) and fluvial systems (Lancaster and Baas, 1998; Maun and Perumal, 1999; Collins *et al.*, 2004; Istanbuluoglu and Bras, 2005). Researchers have also begun to explore feedbacks between macrofauna, vegetation, soil formation and sediment transport. Burrowing animals and plants disturb soil and enhance soil 'creep' thereby regulating soil thickness and hillslope form, providing a feedback mechanism whereby soil development limits the species that inhabit it (Yair, 1995; Gabet *et al.*, 2003; Yoo *et al.*, 2005a, 2005b; Meysman *et al.*, 2006; Roering, 2008; Phillips, 2009).

#### Knowledge gaps

Although several case studies have begun to detail co-evolution between biological communities and landscape formation, we have little understanding of how feedbacks between biology and physics actually work. We have a comparatively decent understanding of how physical processes drive biology but our understanding of how biology influences physical processes is confined to a scattering of case studies that lack a clearly organized conceptual framework. As a result, we have little idea of the spatial and temporal scales at which biology might shift from a cause to a consequence of physical processes (*cf* Schumm and Lichty, 1965) and little idea of how to go about detecting such shifts. There are many examples where biology exhibits a clear effect on physical processes at a small scale, including the binding of river banks and bed substrate by vegetation and biomats (respectively); the burrowing effect of worms, gophers and fallen trees that loosens soil and enhances transport; corals and mangroves dissipating wave energy; vegetation influencing runoff and infiltration; and biogeochemistry causing flocculation of clay particles. It is not clear what the net effect of these processes is at significantly larger time and space scales.

#### Ways forward

In this section we suggest ways in which we can advance our knowledge of co-evolution by asking three questions: (1) Is

there a topographic signature of life and, if so, at what scale(s) is this signature apparent? (2) Is it possible to 'demonstrate co-evolution of life and its landscape?' (3) To what extent does biodiversity influence the evolution of landscapes?

#### Is there a topographic signature of life and, if so, at what scale(s) is this signature apparent?

The first step towards generating an organizing framework is to ask is there a 'fingerprint' of biology on the landscape and, if so, at what scales do patterns that are specifically biogenic in origin manifest themselves? Clear examples of life signatures can be seen in large carbonate systems such as reefs and atolls and in smaller transitional landscapes such as parabolic dunes (Baas and Nield, 2007). It has even been suggested that the existence of granite is indirectly a result of life, through recycling of organic matter into the mantle during subduction (Lee *et al.*, 2008). However, Dietrich and Perron (2006) argued that the overwhelming majority of landforms on Earth, while clearly modulated in their rate of evolution by biological processes, are not clearly biogenic in their origin. They posited that geological processes control biological processes over large spatial scale, whereas biological processes can in turn modify physical processes at much smaller 'local' scales. To the extent this is correct we should be able to detect scale-dependent signatures of life in the statistics of landscape topography. This is exactly what Lashermes *et al.* (2007) and Roering (in prep) found in their examination of 1 m resolution LiDAR elevation data from the Oregon Coast Range. The landscape appeared to be fractal across a wide range of scales (as is common), however, there was clear evidence of a scaling break below 7 m. This scale corresponds to the size of pit and mound features created from fallen trees. Statistical analysis of high resolution topographic data may reveal such scaling breaks in other landscapes. If field work indicates that these breaks are related to known biogenic processes, we will have made a significant conceptual step forward in demonstrating the relevance of biology to landscape form and function, and to quantifying the scales at which these imprints occur. From a numerical modelling perspective, such scale-dependent processes indicate the scale at which coupling between physical and biological processes should be strongest. Direct process modelling of tree growth, tree throw, sediment movement and slope evolution could be carried out at the individual tree scale, and its macroscopic effect on hillslope evolution assessed by time-iterating a spatially extended model, for example.

Another place to search for a signature of life in landscapes is to resolve the temporal evolution of a landscape. While temporal dynamics are more difficult to resolve in slowly evolving landscapes than are spatial patterns, some progress may be made using modelling results as a guide. Recent mathematical modelling of landscape evolution indicates that the presence of vegetation results in more intermittent sediment flux from a drainage basin and leads to steeper hillslope gradients (Istanbuluoglu and Bras, 2005). Analysis of landscape morphology at least partly corroborates these model results, (Tucker *et al.*, 2006; Istanbuluoglu *et al.*, 2008).

#### Can we demonstrate co-evolution of life and its landscape?

We have proposed that the dynamics of life and its landscape are intertwined through a set of feedbacks of differing strength and importance, with co-evolution representing the tightest

coupling between biological and geomorphological systems. Co-evolution may potentially be demonstrated through a combined field and model-testing approach that aims to reconstruct the paleo-dynamics of life and landscape interactions. A first start would be to empirically determine how common co-evolved systems are, which would include attempting to resolve dynamics through reconstructing the trajectory of a landform and its ecological community through time, and using auto-regressive time series models to assess whether there is evidence for temporal feedbacks and dynamic coupling (Ives *et al.*, 2003). In addition, some systems may be amenable to field-scale experimental approaches.

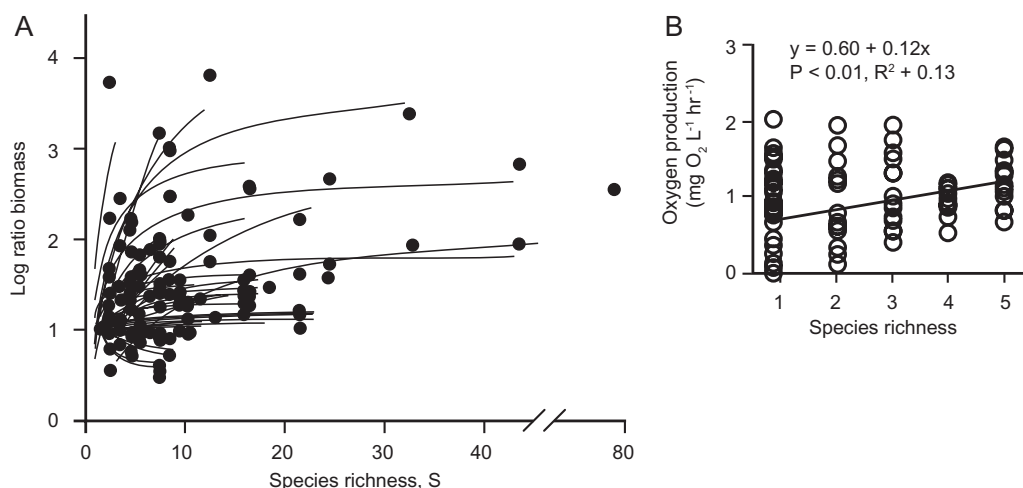
At this early stage of investigation, we believe that the generation of new hypotheses is of key importance. We suggest that simple exploratory models, founded on phenomenology and minimal representation rather than reductionism, be used to investigate life–landscape co-evolution (*cf* Fonstad, 2006). This challenge is distinct from the development of more sophisticated numerical models discussed earlier. We see application of simple models as leading to ‘frontier’ research that will guide more sophisticated investigations in the future. Simple models can direct us towards the types of data we need to collect and experiments to be undertaken in order to test hypotheses.

We may be able to isolate the influence a single species has on a landscape by studying field areas affected by natural extinction or invasion events. Many ecosystems experience rapid loss of the numerically or biomass dominant species due to natural death, disease, or disturbance. Field or remote observations of such events (Ramsey *et al.*, 2005; Pengra *et al.*, 2007) will enable examination of how the loss and replacement of dominant species leads to changes in geomorphological processes. Similarly, invasive species displace native flora and/or fauna, and may have a concomitant effect, and feedback, upon surface processes. Measurement of these interactions may be used to quantify the coupling between life and landscape, and may even offer opportunities to explore how the variety of life influences landscape formation.

To what extent does biodiversity influence the evolution of landscapes?

Earlier we mentioned that laboratory research on bio-physical interactions has, to date, focused on the impacts that individual plant species have on physical processes; similar research on single animal species has been conducted in the field (Gabet *et al.*, 2003; Yoo *et al.*, 2005b; Katija and Dabiri, 2009). Clearly, however, species in nature are seldom found as monocultures. Even some of the least diverse ecosystems on Earth contain dozens, if not hundreds of interacting species. The question we raise here is does this biological variation matter? Can the effects of ‘life’ on physical processes be reasonably condensed into a single parameter that can be used to modify models of physical processes, or do we gain a qualitatively different understanding of natural phenomena by considering the great variation in life that exists on Earth? This is by no means a trivial question. It might be a relatively easy step to modify our understanding about geomorphic processes to consider the role that ‘plants’ play in physics. It would be quite another thing to consider the differing roles that grasses play as opposed to shrubs or trees, and another thing still to consider the roles played by dozens of individual species of grasses, shrubs, or trees (much less the genetic diversity within species populations).

One of the central tenets of ecology is that every species must somehow use biologically limiting resources in a ways that are spatially or temporally unique in order to coexist in nature (Chesson, 2000; Chase and Leibold, 2003). When this is the case, each species should, in theory, have a unique ‘niche’ that imparts a signature on its physical environment. It has been shown that diverse ecological communities composed of many species often produce more biomass per unit area (Figure 5) (Hector *et al.*, 1999; Tilman *et al.*, 2001; Balvanera *et al.*, 2006; Cardinale *et al.*, 2006; Cardinale *et al.*, 2009), and that temporal fluctuations in biomass are smaller in more diverse communities (MacArthur, 1955; Doak *et al.*, 1998; Cottingham *et al.*, 2001; Amarasekare, 2003; Tilman *et*



**Figure 5.** The field of ‘biodiversity and ecosystem functioning’ has shown that many important ecological processes are influenced by the variety of species that comprise a community. (A) Cardinale *et al.* (2006) summarized the results of 55 experiments that have manipulated the species diversity of plants, animals, bacteria or fungi in a controlled setting. They showed that the standing stock abundance or biomass  $Y$  (standardized to species monocultures) of all organisms in a community tends to increase with the number of species  $S$  in the community. Each curve represents data (points) from a single study fit to the function  $Y = Y_{max}S/(K+S)$ , where  $Y_{max}$  is the asymptotic estimate of  $Y$ , and  $K$  is the value of  $S$  at which  $Y = Y_{max}/2$ . The average of all curve fits suggests that the most diverse communities achieve twice the abundance or biomass of an average monoculture ( $Y_{max} = 2$ ), but that individual species can produce at least 50% of the theoretical maximum ( $K = 1$ ). (B) Many physical processes are strongly influenced by the total abundance or biomass of organisms in a community. For example, Power and Cardinale (in press) showed that as species diversity of freshwater algae increases total biomass, it simultaneously increases rates of photosynthesis that control how quickly oxygen is produced and released into water.

*al.*, 2006; Ives and Carpenter, 2008). In part, this results from the fact that species make use of resources in ways that are spatially and temporally unique. To the extent that biomass impacts physical processes that shape a landscape, and the diversity of life regulates the amount and stability of biomass, then it follows that the functional diversity represented by different species would play an important role in modulating and responding to landscape evolution across scales. This is not to say that we must consider the functional role of each and every species, as there is certainly some level of diminishing return in the explanatory power and generality of such complex models. On the other hand, ecology has clearly shown that we can't simply assume that different species of grasses, shrubs, or trees all have similar impacts on their environment, and thus plants cannot all be condensed into a single parameter used to model the influence of 'life' on physical transport processes. What we don't yet know is what level of biological variation matters. How many different types of species or functional groups must we consider to get realistic models? This is an open question worthy of further study.

## Humans as Modifiers of the Landscape

The present rate of Earth-surface evolution is more rapid than at any time since the end of the last ice age, and perhaps even longer. Humans are now the dominant geomorphic agent shaping the surface of the Earth; our activities erode, transport and deposit more material than any other surface process, including past (Pleistocene) glaciations (Hooke, 2000; Wilkinson and McElroy, 2007). It is also estimated that ~50% of Earth's terrestrial ecosystems has been directly transformed or degraded by humanity (Vitousek *et al.*, 1997; Zakri, 2008). Unfortunately, the pace at which Earth's environment is changing also appears to be accelerating (Meyer and Turner II, 1992; Walker *et al.*, 1999). Thus it is axiomatic that we cannot understand landscape dynamics without considering human interactions with other bio-physical processes (*cf* Tansley, 1935). In this section we review the little we know of how human-driven climate change may impact landscapes, discuss how we may improve this knowledge and make predictions, and finally how the science of landscape restoration can be advanced in light of our explicit acknowledgement of the importance of bio-physical interactions.

### The impact of climate change on a landscape

There is little doubt that human-induced climate change is causing both a persistent change in temperature and rainfall, and increases in the frequency and/or magnitude of fluctuations superimposed on that trend (IPCC, 2007). Climate change is also causing a major reduction of biodiversity (Vitousek *et al.*, 1997; Zakri, 2008), changes in biogeochemical cycling (Piao *et al.*, 2008), disease epidemics (Pounds *et al.*, 2006) and direct changes in physical processes through increased storm activity (Emanuel, 2005), flooding (Milly *et al.*, 2002) and drought (Seager *et al.*, 2007). These changes represent perturbations to landscape functioning.

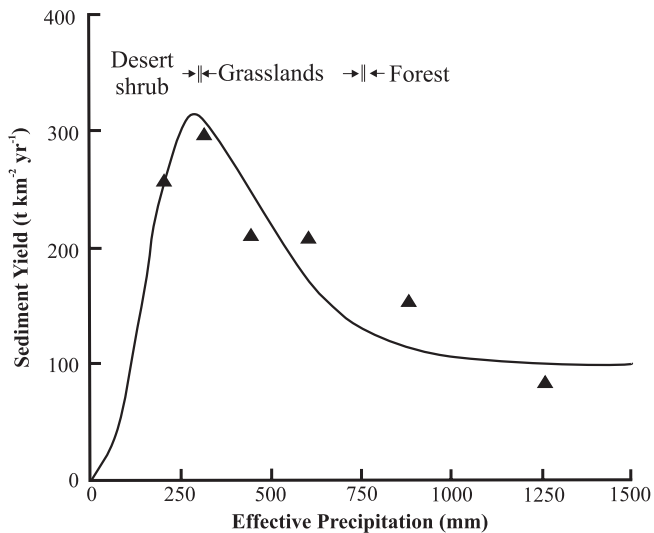
#### State of the art

To date there have been few joint efforts to examine the effects of climate change on landscapes from a coupled ecology-geomorphology perspective. This perspective appears to be best established in coastal studies. Sea level rise will directly impact sediment transport (FitzGerald *et al.*, 2008), but may

also force changes in biological communities. Vegetation growth in salt marshes strongly enhances the stability of bed elevations responding to sea level change. Conversely, episodic disturbance to vegetation can trigger widespread channel erosion, causing marsh vegetation to be permanently lost – an effect that is greater under higher rates of sea level rise (Kirwan *et al.*, 2008). External disturbances and bioturbation, leading to the disruption of the stabilizing polymeric biofilms produced by benthic microbes, may lead to the demolition of tidal flats which would be accreting in the presence of microphytobenthos, and to a catastrophic shift towards a subtidal platform equilibrium (Marani *et al.*, 2007). In strongly coupled (coastal and desert) aeolian environments, changes in vegetation structure may expose relic dune landscapes to erosion, and this, along with changes in wind strength and transport capacity, may evoke nonlinear feedbacks and reactivate areas such as the Great Plains (Muhs and Holliday, 1995) and Southern Africa (Thomas *et al.*, 2005).

Earlier we discussed how diverse ecological communities composed of many species often produce more biomass per unit area and appear to be more stable than less diverse communities (Figure 5). Biodiversity also appears to regulate the amount of mortality imposed on a community by environmental fluctuations (Doak *et al.*, 1998; Tilman and Downing, 1994). This observation leads us to hypothesize that a high diversity of species in a habitat may also have a stabilizing effect on the physical landscape as well. An important corollary of this hypothesis is that a reduction in biodiversity can destabilize a landscape. This is not to say that in some systems – such as those structured by keystone or foundational species – the loss of one species might be sufficient to induce catastrophic change. However, destabilization is likely to be a consequence of biodiversity loss *per se* because the functional diversity of organisms moderates physical processes such as river bank erosion (Tal and Paola, 2007), soil creep (Yoo *et al.*, 2005b), air flow (Baas and Nield, 2007) and water infiltration (Van Peer *et al.*, 2004). A uniquely biotic illustration of such destabilization are wildfires, which promote rapid, stochastic erosion events that strongly influence hillslope stability and carbon cycling (Roering and Gerber, 2005; Bond-Lamberty *et al.*, 2007).

There is a consensus that climate-driven changes in precipitation will influence the pattern and type of vegetation (and animals) in landscapes, which will in turn influence physical processes. In a simple (simplistic?) sense vegetation acts as a protective cover: the canopy reduces rain-splash while roots bind soil and protect it from erosion. This relationship is described by the Langbein and Schumm (1958) curve, which predicts that the landscapes most sensitive to changes in precipitation are semi-arid to arid environments (Figure 6). Unfortunately, this simple relationship is based on <100 years of field data and appears to only hold true in a continental climate (Walling and Webb, 1983). More recent field studies have shown that there is no direct relationship between *mean* annual temperature or precipitation and catchment erosion over millennial timescales (von Blanckenburg, 2005). Instead it seems likely that short-term fluctuations in biological and physical processes are more important than any average activity (e.g. flood variability). In other words we argue here that the key factor mediating landscape response to climate change is variability in biological and physical processes. An obvious example of how short-term climate-driven biotic variability can drive long-term landscape evolution is through the wildfires mentioned above. Another important example is the effect of short-term fluctuations in river discharge (i.e. floods) on the long-term evolution of rivers. Flood variability is largely dictated by precipitation pattern, though there is striking evidence



**Figure 6.** The relationship between Sediment yield effective precipitation in the continental USA. (Langbein and Schumm, 1958). In areas with effective precipitation in excess of 300 mm vegetation growth protects the underlying surface. Data (triangles) are averaged from 94 stream sampling stations. Effective precipitation is defined as the annual precipitation required to generate annual runoff at 50°F.

that biological mechanisms such as deforestation also accelerate flooding (Bradshaw *et al.*, 2007). This matters greatly because flooding is the principal mechanism by which rivers incise and transport sediment (Baker, 1977; Wolman and Gerson, 1978; Baker and Pickup, 1987; Kochel, 1988; Wohl, 1992; Gintz *et al.*, 1996; Baker and Kale, 1998; Howard, 1998; Sklar and Dietrich, 1998, 2004); rivers in turn set the pace of landscape evolution by (1) controlling sediment efflux through a valley and (2) setting the base-level to which hillslopes respond. Thus any increase in precipitation (or climate driven changes in biota) may have a profound impact upon river dynamics and the surrounding landscape (Tucker, 2004).

#### Knowledge gaps

The striking internal dynamics of ecological and geomorphic systems inhibit our ability to predict how landscapes may respond to climatic perturbations. This inherent variability is often of similar magnitude and frequency to externally forced disturbances such as climate change (Jerolmack and Paola, 2007; Kim and Jerolmack, 2008). For example, river valley-scale erosion rates are highly variable in time, as measured from cosmogenic nuclides (von Blanckenburg, 2005) and inferred from the depositional record downstream of such catchments (Jerolmack and Sadler, 2007). Often these large fluctuations are attributed to changes in uplift or rainfall, however, there is mounting evidence that most sediment transport systems exhibit fluctuations over a wide range of scales resulting from the nonlinear threshold dynamics of sediment transport. Physical experiments have shown large variability in transport rates under steady conditions for bed forms (Gomez and Phillips, 1999; Singh *et al.*, 2009), braided rivers (Ashmore, 1982) and deltas (Kim *et al.*, 2006; Kim and Jerolmack, 2008). We expect similar behaviour from soil transport down hillslopes and river incision, especially since landslide distributions in nature are known to be heavy-tailed (i.e. power law; Stark and Hovius, 2001; Malamud *et al.*, 2004). Given these internal dynamics it is entirely possible that some perturbations imposed by climate change will be lost within the general system noise and thus have little measurable impact on a landscape: to-date this issue remains relatively unexplored.

Assuming that external climate driven perturbations are large enough, or of the proper frequency, to initiate a change in landscape dynamics then the response of these nonlinear systems is likely to be complex. We use the term 'complex' advisedly as nonlinear interactions between physical process and biological activity are thought to lead to self-organization and the development of emergent landforms (Werner, 1999; Murray, 2007; Murray *et al.*, 2008). If real-world landscapes do exhibit complex behaviour then the final (emergent) form of a landscape perturbed by climate may not be predicted from small-scale processes (i.e. a purely reductionist approach will not work). Instead, prediction would require explicit modelling of the coupling between physical and biological processes over broad spatial scales; implying that modelling at an appropriate spatial scale (rather than the finest possible scale) is likely far more important than accurate description of each biotic and abiotic process.

#### Ways forward

Climate change is perhaps THE grand challenge of our time. The Intergovernmental Panel on Climate Change is continuously revising its predictions for expected warming and extreme events, and we are entering an era where regional climate predictions are becoming possible (IPCC, 2007). Whether or not landscapes can 'keep up' with climate change, in the sense that landscapes remain fairly stable, likely depends on both physical and ecological factors and their coupling. Determining landscape susceptibility to destabilization induced by climate change is imperative for limiting human and ecological losses. Our community should be in a position to offer policy-relevant prediction of landscape response to climate change through the coupling of Global Circulation Models and geomorphic models. We make the following suggestions to advance our predictive ability:

1. We hypothesize that the sharpest climatic gradients and interfaces in landscapes are the most sensitive to the effects of climate change. The margins of continents, glaciers and arctic and desert areas are likely to be the regions most sensitive to climate change. One of the most obvious examples is in high-altitude regions where permafrost melting and migrating biomes create opportunities for rapid ecological change. Such ongoing climatically-driven changes in landscape may be viewed as vast experiments in which key bio-physical feedbacks could potentially be identified, studied and modelled.
2. Explicit recognition of process thresholds is necessary to predict landscape sensitivity and to determine whether exceedence of these thresholds could lead to catastrophic destabilization of a landscape. Examples of process thresholds include: critical moisture and temperature to sustain vegetation (desertification); critical temperature to sustain permafrost; critical sea-level rise rate that biota (corals, salt marshes, mangroves) can keep up with; and critical erosion or deposition rates that may trigger large-scale shifts in landscape morphology. Acquiring data on simultaneous landscape and ecological change would allow us to catalogue thresholds potentially enabling generation of a map of susceptible landscapes.
3. Some smaller-scale, direct human intervention in landscapes may perhaps serve as an analogue for climate change. For example, rapid rise of water level in a man-made reservoir may be analogous to climate-induced sea level rise, or the heat effect of urban areas may be similar to climate-induced warming. These cases should be studied in the context of life and landscape response to climate change.

4. Paleo-records of past climate change and landscape response can also be used to infer future possible changes, as well as providing boundary conditions for development and validation of simulation models (Dearing, 2006).

### Long-term sustainability of human-influenced and human-occupied environments

Global environmental change has been directly and indirectly driven by growth in the human population and economic development, which has accelerated resource consumption, economic activity and urbanization. Mining and construction have an important influence upon landscape dynamics but agriculture is the dominant human 'process': agriculture accounts for ~70% of human transported material while occupying only ~37% of the global ice-free land surface (Wilkinson and McElroy, 2007).

#### State of the art

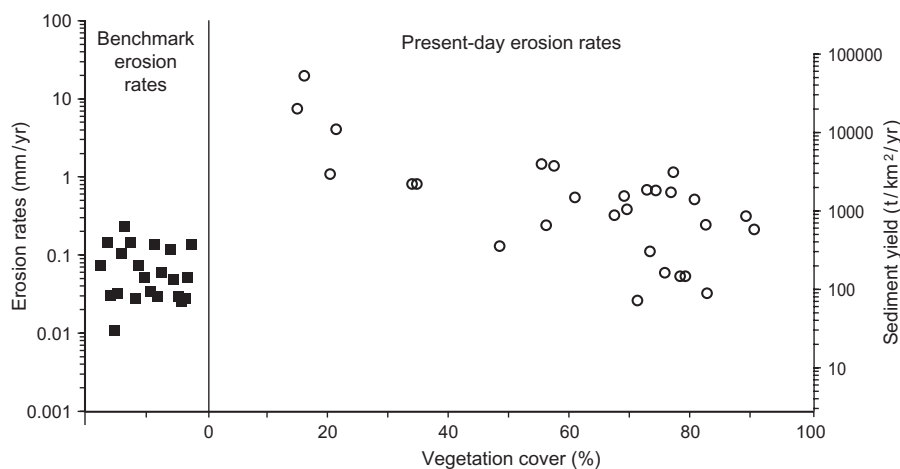
Direct anthropogenic disturbance of natural environments may be much larger in many places than the (projected) indirect effects of climate change. It is now established that land use changes can accelerate natural erosion processes by up to 100 times (Figure 7) (Hewawasam *et al.*, 2003; Vanacker *et al.*, 2007). Anthropogenic impacts on soil erosion and the consequent landscape evolution have long been appreciated. Ancient Greek and Roman writers reported examples of human environmental impacts, including land degradation, thinning of soils and silting up of harbours (e.g. Ephesus and Miletus). Possibly the most famous case of accelerated soil erosion resulting from human actions was the North American 'dust bowl' of the 1930s. The devastating effect of the 'black blizzards' drew large public and scientific attention to the effects of humans on accelerating soil erosion. As a consequence of this ecological disaster large-scale US governmental programmes for soil conservation were implemented. The Soil Conservation Service and the Agricultural Research Service focused their efforts on quantifying the impact of different land use practices, and they developed the so-called Universal Soil Loss Equation (USLE, Wischmeier and Smith, 1978). This research field developed rapidly, and many empirical and modelling studies have quantified the impact of human activ-

ity on erosion (see reviews in Goudie, 2005). More recently the Global Land Project was established (in 2005) to measure, model and understand the coupled human-environmental system: it is part of the International Geosphere-Biosphere programme.

#### Knowledge gaps

Notwithstanding the growing number of field studies on the effect of land use change on erosion rates, quantitative information on the importance of humans as agents of erosion and landscape morphology is scarce. Most field studies have concentrated on agricultural land in temperate environments with gentle to low-relief, as these areas are of primary importance for the global food production. Although human-accelerated rates of soil erosion can be high for some of these agricultural parcels, it is certain that these areas are only of limited importance for global sediment delivery (Syvitski *et al.*, 2005). The lack of knowledge is particularly important in tropical mountain regions where large rivers act as great conveyor belts that efficiently carry more than half of the global sediment flux to the oceans, along with a great deal of organic carbon. Burial of organic carbon 'represents the second largest atmospheric CO<sub>2</sub> sink (after silicate weathering coupled to carbonate precipitation) and contributes to long-term climate regulation' (Berner, 1990; Galy *et al.*, 2007, p.407). Many areas in the tropics are undergoing very rapid change at present due to a rapid increase in population and dramatic changes in agricultural practices. The impact of these accelerated land use changes on erosion, sediment transfer and landscape evolution is not only an important scientific gap, but has also practical implications: declining agricultural productivity by accelerated soil erosion can limit the prospects for future socio-economic development (Montgomery, 2007).

The standard tools to determine soil erosion rates are sediment measurements using a comparative plot or field approach. However, this approach does not allow one to assess the impact of humans on erosion processes occurring at the catchment scale. Sediment fluxes are known to be of an episodic nature, and conventional sediment-yield measurements can greatly underestimate or overestimate long-term average sediment flux rates (Kirchner *et al.*, 2001). Fortunately, new methods and tools such as cosmogenic nuclides allow us to 'average out' short-term fluctuations in sediment fluxes, and



**Figure 7.** Field data on the acceleration of erosion by humans from the Southern Ecuadorian Andes. Long-term natural benchmark rates of erosion were derived from cosmogenic nuclide concentration in river sediment. These erosion rates are compared with present-day erosion rates extracted from reservoir sedimentation rates. The data indicate that land cover change can accelerate erosion rates by up to 100 times. Surface vegetation cover strongly controls catchment-wide erosion rates, which decrease exponentially with an increasing fractional vegetation cover of the catchment.

provide erosion rate benchmarks against which anthropogenic or climate-induced changes in erosion can be evaluated (Hewawasam *et al.*, 2003). A comprehensive study on erosion rates from agricultural fields under conventional agriculture and geologic rates of erosion by Montgomery (2007) showed that conventionally plowed fields generally erode at rates typical of alpine terrain under native vegetation. However, land use change is not only the cause but can also be the consequence of erosion processes (Bakker *et al.*, 2005). These feedbacks between human activities, land use and their environment are rarely studied holistically.

Despite the developing body of empirical studies and new techniques such as cellular models (Coulthard *et al.*, 2007; Nicholas and Quine, 2007), few attempts have been made to integrate human impacts in landscape evolution models. So far, most modelling approaches use scenarios of varying complexity to link human activity to landscape evolution. The main drawback of using static scenarios for landscape evolution modelling is that they fail to take into account dynamic interactions and feedback mechanisms, which can lead to the simulation of totally unrealistic conditions (Wainwright, 2008). Predicting the response of human society to management scenarios requires explicit consideration of human-landscape coupling, and the nonlinearities that may arise from this coupling.

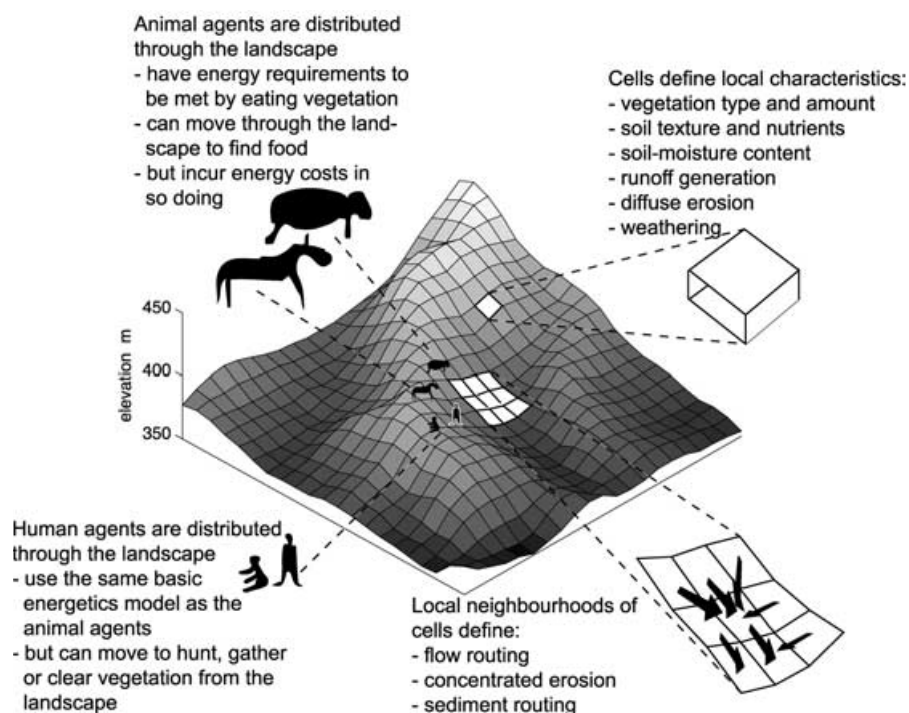
#### Ways forward

Agent-based models that accommodate the complex interplay of humans (and animals) and their environment have recently been developed (Wainwright and Mulligan, 2003; Li An *et al.*, 2005; Werner and MacNamara, 2007; McNamara, and Werner, 2008a; Wainwright, 2008). Most examples using agent-based models in the broader field of geosciences are those that link agent decisions to a cellular model for land use and cover change (Parker *et al.*, 2003). While these types of examples are promising, the scope of these models does not

include process-based landscape dynamics nor does it include instances of strong coupling between human interactions and natural landscape dynamics. In order to address these issues, more recent attempts have coupled models for economic markets – composed of bounded rational agents whose decisions are made using prediction models – to models for natural landscape dynamics (McNamara and Werner, 2008a; Werner and McNamara, 2007). An example of one agent based modelling framework is shown in Figure 8.

The utility of this agent-based approach is that it provides a modelling framework that can be used to explicitly model human and animal interactions with the natural landscape (O'Sullivan and Haklay, 2000; Wainwright and Mulligan, 2003). They include the capability of responding in non-trivial ways to a complicated and changing external (natural) and internal (other agents) environment. This allows for the possibility of rich nonlinear behaviour such as foraging (Li An *et al.*, 2005), herding (Arthur *et al.*, 1997), multiple stable states (DeCanio, 2003) and emergence in the coupled human landscape system (Liu *et al.*, 2007; McNamara and Werner, 2008a; Wainwright, 2008); characteristics often lacking in more traditional approaches to simulating human interactions in natural systems such as regression techniques and integrated assessment models. At present the rigid rules governing agent based models allow minimal flexibility for adaptability to longer term changes. Investigations are now underway to allow agents to evolve by learning directly from their environment and from each other; effectively allowing them to reformulate the rules that guide their behaviour and adapt to long-term changes (Wainwright, 2008).

As there are many bio-physical systems in which humans play a first-order role in altering landscape functioning future developments using agent-based models should be directed toward modelling human interactions in such systems. Examples might include models for coupled groundwater reservoir extraction and natural groundwater flow, or coupled



**Figure 8.** General structure of the CYBEROSION agent-based modelling framework. This model employs a cellular representation of a landscape based on a digital elevation model (DEM) of the topography. It aims to reproduce the key interactions between the landscape, vegetation, animals and people (Wainwright, 2008).

urban development and hillslope evolution in fire prone regions. Agent-based model developments should also focus on investigating strategies other than maximizing profit for driving human interactions with the natural landscape. For example, it has been suggested that increasing concern about human impacts to climate may lead to alternate strategies for managing carbon emissions (Dessler and Parson, 2006) and such strategies may play a role in driving landscape interactions. Broader developments for agent-based models in landscape systems could include addition of long timescale dynamics associated with adaptation in agent behaviour that would allow models to explore evolution of strategies that drive human interactions with the landscape. Future needs for agent based models in landscape systems are driven mostly by new dynamical variables used in characterizing human landscape systems that now necessitate new methods for data collection or new analysis of existing data sets so that models can be adequately tested (McNamara and Werner, 2008b).

We have already discussed the need to develop physical experiments, alongside numerical models. This is crucial if we are to determine the scales of interaction between physical and biological processes. Physical and biological systems operate across multiple scales, and *complex* nonlinear interactions between physical process and biological activity are commonly observed. Spatial nonlinearities and emergent structures challenge our ability to understand and predict system behaviour at one scale based on information obtained at finer or broader scales (Peters *et al.*, 2004). For example, broad-scale physical drivers (such as river hydraulics) often have limited ability to explain floodplain building at finer scales that is controlled by local processes such as vegetation colonization (*cf* Tal *et al.*, 2007). Physical experiments should serve as a test bed for the identification and analysis of cross-scale feedback-driven interactions in natural, human-influenced and human-occupied environments. Results from physical experiments must be integrated with numerical and field based data; rapid cycling among all three elements of this triad is needed to synthesize insights into complex system behaviour and emergent landforms.

## Ecological management and landscape restoration

Restoration of degraded or altered landscapes is often carried out with ecological goals in mind. The tools of restoration, however, are generally physical, e.g. modification of the physical landscape to reduce erosion or to alter the flux of water through the surface or subsurface. Unfortunately, most restoration projects (90%) are not monitored after they have been completed and we have no robust data on the proportion that are successful (Bernhardt *et al.*, 2005), though there is anecdotal evidence to suggest that more than 50% fail to meet their design objectives. One obvious difficulty for restoration is that physical construction of habitat does not necessarily result in organisms entering the ecosystem. More broadly, we speculate that many failures are due to unknown or poorly understood bio-physical feedbacks (*cf* Palmer and Bernhardt, 2006; Bernhardt *et al.*, 2007).

### State of the art

Traditionally, restoration is seen as a means to halt degradation and to redirect the development of a degraded ecosystem towards a desired state that resembles the conditions presumed (or known) to have prevailed prior to the onset of degradation (Aronson *et al.*, 1993; Dobson, 1997; Choi *et al.*, 2008). A continuum of restoration efforts can be recognized

ranging from restoration of localized highly degraded sites to restoration of entire landscapes for production and/or conservation reasons. In each case, restoration aims to return the degraded or altered system to some form of more sustainable or ecologically integrated land management. While the tools and the techniques that are used in specific restoration actions can be very different, the key principles in restoration are fundamentally similar. Hobbs and Norton (1996) have emphasized the importance of developing restoration methodologies that are generally applicable at the landscape scale. They identified four processes that are key for the successful integration of restoration into sustainable land management: (i) identifying and tackling processes leading to degradation or decline; (ii) determining realistic goals and measures of success; (iii) developing methods for implementing the goals; and (iv) monitoring key system variables to assess progress of restoration actions. While the first generation of restoration projects often proceeded without initial identification and/or amelioration of the processes causing degradation, recent actions increasingly tend to include these generic procedures (e.g. Everglades restoration efforts).

### Knowledge gaps

It is commonly accepted that restoration seeks to return some aspects of natural ecosystems function to degraded systems. Often, however, the system will not respond directly to the removal of the degrading influence and will need some other intervention to facilitate restoration. This is particularly true for ecosystems that have crossed a specific (often unknown) ecological threshold, and where removing the stressor will not be sufficient to allow transition towards a more desired ecological state. This situation has been observed in Badland topography that developed following decades of unsustainable agricultural practice (Vanacker *et al.*, 2003a): in these degraded landscapes, soil material has been stripped off making it difficult for plants to re-colonize. Without human intervention restoration of such landscapes is extremely slow and perhaps impossible over a human timescale.

In the past, many restoration projects have set far too ambitious goals, and claimed to re-establish the 'natural' ecological conditions that resemble the state of native ecosystems. The idea of restoring native ecosystems is increasingly challenged, as 'natural' communities and ecosystems are extremely rare in our modern world (Vitousek *et al.*, 1997). Furthermore, the environment is continuously changing and it would be naive to think that we can restore a specific historical situation. Beyond the naivety of such an approach there is also the difficulty of targeting a particular outcome: as we discussed earlier, landscape response to disturbance is often nonlinear making prediction difficult (*cf* Lorenz, 1963; Scheffer *et al.*, 2001; Phillips, 2006).

### Ways forward

Restoration design must move towards the dynamic view of an evolving landscape forced by both geomorphological and ecological feedbacks. We see opportunities to rapidly advance the theory behind restoration through detailed post-project monitoring of the physical and biological landscape response to ongoing restoration projects. In this context ongoing restoration projects can be viewed as large-scale field experiments where the effect of disturbances on physical, biological and ecological functions and services can be evaluated. At the moment, monitoring of restoration programmes is rare. It is clear that this is a missed chance: careful monitoring of various ecosystem attributes before, during and after the restoration actions is likely to provide key insights in complex feedback mechanisms in ecological systems. It is axiomatic that

pre-restoration design and post-restoration monitoring requires close collaboration among ecologists and geomorphologists.

To evaluate restoration programmes, it is crucial to develop a clear set of thoughtfully defined criteria for measuring success in ecosystem restoration (Zedler, 2001). Less obvious, however, is how success criteria should be measured. Some authors suggest using similarity indices between the ecosystem attributes (structure, function, composition) of the restored system and some reference system, while others prefer to use indicator taxa (Verdonschot, 2000; Jenkins and Boulton, 2007). Alternatively, numerical scorecards are proposed as a means to quantify the effect of restoration efforts on multiple ecosystem attributes and functions (Koch and Hobbs, 2007).

Finally, restoration science needs to become prescriptive rather than descriptive. To achieve this requires continued use (and advance) of physical and numerical experiments as an integral part of restoration schemes (see earlier sections for review of these techniques). Determination of the scales of interaction between physical and biological processes is key to predicting how they interact. For example, determining the characteristic timescales of vegetation colonization and growth, and floodplain accretion, would allow one to infer cross-scale interactions and feedbacks in river floodplain building. Integrated model approaches will be necessary to synthesize the empirical insights into this complex system behaviour. Integrated modelling of nonlinear interactions and emergent behaviour will necessitate modelling at different levels of abstraction and at multiple spatial and temporal scales, alongside both 'top-down' and 'bottom-up' approaches. These approaches will need to engage with the rapidly developing fields of complex systems and agent-based modelling.

## Conclusion

We have proposed that the dynamics of life and its landscape are intertwined through a set of feedbacks of differing strength and importance; with co-evolution representing the tightest coupling between biological and geomorphological systems. Co-evolution involves 'feedbacks in which the physical environment regulates the numbers and types of organisms that can coexist in a community and shape the selective environment that drives evolution while, at the same time, the organisms themselves modify the environment in a way that enhances their own persistence.' An extension of this proposition is that 'biological variation matters' to landform development, as species tend to modify and/or create habitat in ways that enhance their own survival and/or the existence of other species. What we don't yet know is what level of biological variation matters. How many different types of species or functional groups, and what physical processes over what scales must we consider before we can understand and predict landscape functioning and response to perturbations such as climate change? We advanced three key questions, alongside potential solutions, that serve as a guide towards answers: (1) Is there a topographic signature of life and, if so, at what scale(s) is this signature apparent? (2) Can we demonstrate co-evolution of life and its landscape. (3) To what extent does biodiversity influence the evolution of landscapes?

Questions of landscape functioning and feedbacks can rarely be considered without inclusion of human activities. Humans are the dominant geomorphic agent shaping the surface of the Earth and the primary agent of ecological change. We have achieved this dubious distinction through direct actions such as agriculture and indirectly through modification of atmospheric composition and biogeochemical

cycles. There is a growing consensus that increasing greenhouse gas concentrations and concomitant changes in climate will influence the pattern and type of flora and fauna in landscapes, which will in turn influence physical processes. Physical processes will also be directly modified through changes in precipitation (among other factors), as flooding is the principal mechanism of sediment transport and river incision. Predicting how climate driven changes in biotic-abiotic interactions may transform landscape functioning is extremely problematic. We posit that the key factor driving landscape response to climate change is variability in biological and physical processes. Notwithstanding this insight it remains unclear whether externally forced disturbance due to climate change will be of sufficient magnitude and/or frequency to exceed the high degree of natural variability extant in most landscapes. Assuming that external climate driven perturbations are large enough in magnitude and frequency to initiate a change in landscape functioning, then the response of these nonlinear systems is likely to be complex (in a formal sense). We hypothesize that landscapes that exhibit a tight coupling of physical and biological processes, and whose form is thus controlled by this coupling, will be most susceptible to destabilization due to climate change.

Whether or not landscapes remain stable in the future depends on both physical and ecological factors and their coupling. We reviewed the state of the art in numerical and physical modelling and argued that new numerical models that explicitly integrate (dynamically interacting) biological and physical processes over the timescales of plant and human life are needed. A new class of physical model has successfully achieved this dynamism for single species interactions but modelling multi-species ecological-level interactions remains problematic: effective use of field-scale experiments offer a solution to this problem. Choosing appropriate scales for numerical models is often problematic. It should be possible, at least in some cases, to identify the dominant spatial and temporal scales at which ecology influences geomorphology; these should be the fundamental scales for numerical models. In addition, agent- or actor-based numerical models appear capable of accommodating at least some of the complex interplay between humans and their environment. We also discussed the need to improve the science of landscape restoration. Few restoration projects are monitored after they have been completed (~10%) and there is anecdotal evidence that as many as half fail to meet their design objectives. We argue that the theory behind restoration can be rapidly advanced through detailed post-project monitoring of the physical and biological landscape response to ongoing restoration projects. In this context ongoing restoration projects can be viewed as large-scale field experiments where the effect of disturbances on physical, biological and ecological functions and services can be evaluated.

Over the medium to long term we propose that our community aim to offer policy-relevant prediction of landscape response to climate change through the coupling of Global Circulation Models and geomorphic models. We advanced a number of suggestions that may bring us closer to this goal: these include: (1) more studies in marginal areas that have the sharpest climatic gradients and interfaces and are thus most sensitive to the effects of climate change; (2) explicit recognition of process thresholds, necessary to predict landscape sensitivity and to determine whether exceedence of these thresholds could lead to catastrophic destabilization of a landscape; (3) development of simplified models to identify potential (nonlinear) bio-physical feedbacks – once identified these feedbacks could be incorporated in more sophisticated models; (4) strengthening of the connection between field/



laboratory observations and physical and numerical modeling efforts with rapid cycling among all three elements of this triad; and (5) agreement upon a suite of spatial and temporally sensitive tests of model output. These tests should allow for a hierarchical scale of model 'validations' of differing strength. Inclusion of ecological dynamics, which operate on relatively short timescales, may provide new temporally sensitive tests.

In this review we have suggested that life and landscape are often so intimately connected that they cannot be separately treated. This is not always true, of course, and identifying when and how bio-physical feedbacks are important remains frontier research. While significant progress has been made on isolated pieces of this puzzle, what must be done is to assemble these pieces to better understand the structure and evolution of landscapes. This task lies at the interface of geomorphology and ecology. A holistic Earth Surface Science that combines the best analytical approaches from both disciplines is necessary to enable quantitative prediction of Earth-surface response to climate change and human disturbance. There are considerable challenges but also opportunities in developing a more comprehensive Earth Surface Science; disciplinary and language divides still present real obstacles to progress, however life-landscape investigations also broaden the scope and significance of our research. It is encouraging that dialogue between geomorphologists and ecologists is more and

more common. It is our hope that this review will help to facilitate this dialogue, by pointing a way toward fruitful avenues of collaboration.

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