

Linking ecological theory with stream restoration

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SUMMARY

1. Faced with widespread degradation of riverine ecosystems, stream restoration has greatly increased. Such restoration is rarely planned and executed with inputs from ecological theory. In this paper, we seek to identify principles from ecological theory that have been, or could be, used to guide stream restoration.
2. In attempts to re-establish populations, knowledge of the species' life history, habitat template and spatio-temporal scope is critical. In many cases dispersal will be a critical process in maintaining viable populations at the landscape scale, and special attention should be given to the unique geometry of stream systems
3. One way by which organisms survive natural disturbances is by the use of refugia, many forms of which may have been lost with degradation. Restoring refugia may therefore be critical to survival of target populations, particularly in facilitating resilience to ongoing anthropogenic disturbance regimes.
4. Restoring connectivity, especially longitudinal connectivity, has been a major restoration goal. In restoring lateral connectivity there has been an increasing awareness of the riparian zone as a critical transition zone between streams and their catchments.
5. Increased knowledge of food web structure – bottom-up versus top-down control, trophic cascades and subsidies – are yet to be applied to stream restoration efforts.
6. In restoration, species are drawn from the regional species pool. Having overcome dispersal and environmental constraints (filters), species persistence may be governed by local internal dynamics, which are referred to as assembly rules.
7. While restoration projects often define goals and endpoints, the succession pathways and mechanisms (e.g. facilitation) by which these may be achieved are rarely considered. This occurs in spite of a large of body of general theory on which to draw.
8. Stream restoration has neglected ecosystem processes. The concept that increasing biodiversity increases ecosystem functioning is very relevant to stream restoration. Whether biodiversity affects ecosystem processes, such as decomposition, in streams is equivocal.
9. Considering the spatial scale of restoration projects is critical to success. Success is more likely with large-scale projects, but they will often be infeasible in terms of the available resources and conflicts of interest. Small-scale restoration may remedy specific problems. In general, restoration should occur at the appropriate spatial scale such that restoration is not reversed by the prevailing disturbance regime.
10. The effectiveness and predictability of stream ecosystem restoration will improve with an increased understanding of the processes by which ecosystems develop and are maintained. Ideas from general ecological theory can clearly be better incorporated into stream restoration projects. This will provide a twofold benefit in providing an opportunity both to improve restoration outcomes and to test ecological theory.

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Introduction

Of all types of ecosystems, those of flowing waters are amongst the most damaged by human activities (Sala *et al.*, 2000). Flowing waters are especially susceptible to degradation as their channels and floodplains have been directly damaged, but streams have also been indirectly damaged by activities being carried out in their catchments. With the increasing awareness of the economic, ecological and social losses arising from stream degradation, pressures to conserve and restore flowing waters have gathered strength in recent times (Palmer *et al.*, 2004; Bernhardt *et al.*, 2005; Dudgeon *et al.*, 2006). In North America, Europe, Japan and Australasia, large sums of money have been spent on restoration, with stream and river restoration becoming a major part of environmental policy (e.g. White, Rutherford & Hardie, 1999; Bernhardt *et al.*, 2005).

Most stream restoration projects are small-scale, one-offs involving localised interventions in stream channels, riparian zones and floodplains (Bond & Lake, 2003b; Bernhardt *et al.*, 2005). Rarely do they involve extensive interventions at the catchment scale addressing such activities as land use. This is reflected in the lack of large-scale catchment restoration projects (Holl, Crone & Schultz, 2003). Furthermore, most projects are either not monitored or are poorly monitored (Bernhardt *et al.*, 2005) and in those projects with monitoring, it is often the implementation measures rather than the ecosystem responses to restoration that are followed. If information is sought to guide the project, it is usually technical information–implementation measures ('the cook book myth'; Hilderbrand, Watts & Randle, 2005), rather than information on response monitoring.

The focus on implementation and practice in stream restoration has occurred at the expense of using ecological concepts and theory, which have apparently been much more influential in guiding restoration in terrestrial environments (viz. Hobbs & Norton, 1996; Holl *et al.*, 2003), wetlands (Middleton, 1998; Zedler, 2000), and lakes (Carpenter & Lathrop, 1999; Drenner & Hambright, 1999) than in flowing water systems. While particular principles from stream ecology have been used to guide restoration, such as

the need for particular configurations of physical habitat for appropriate flow regimes and for connectivity (Ward *et al.*, 2001), the incorporation of theories and principles derived from basic ecology have been rarely drawn upon.

Stream restoration projects in turn offer an opportunity setting in which to test a multitude of ecological theories, including ideas on population dynamics, of community assembly and persistence, and of ecosystem structure and function. A larger and potentially more enlightening challenge lies in identifying those ecological theories or parts of theories that can increase and improve our understanding of the ecology of stream restoration. Thus, this paper seeks to identify some aspects of ecological theory (including from stream ecology) that have been applied to stream restoration, as well as to highlight some aspects of ecological theory that can be used to improve the effectiveness of stream restoration. We concentrate on streams in rural and natural settings, though we realise that urbanisation as a force in changing land use and hydrology is steadily increasing its range (Paul & Meyer, 2001; Nilsson *et al.*, 2003).

Habitat restoration and life history

Restoration of populations of single species or a targeted group of species is a common aim of stream restoration. For single species, it is very advisable to have a good understanding of the life history, the habitat template (the characteristics of the species habitat in terms of temporal and spatial heterogeneity; Southwood, 1977) and the scope (the maximum and minimum spatial extent and temporal duration; Schneider, 1994) of the target species. The latter point brings in the need for stream connectivity to allow movement of the target species over the appropriate spatio-temporal scales. For example, a project in Victoria, south-east Australia, has aimed at restoring native fish populations, including western carp gudgeons (*Hypseleotris klunzingeri* Ogilby) and mountain galaxias (*Galaxias olidus* Günther), in stream sections degraded by excessive sedimentation by sand (Bond & Lake, 2003a, 2005a,b). In the target system, differences in the life-history dynamics (in particular upstream spawning movements by galaxiids) means

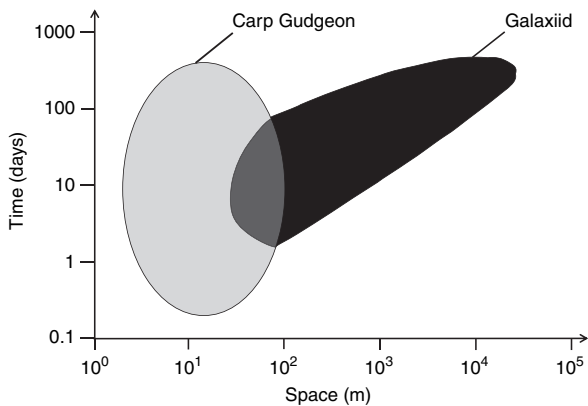


Fig. 1 Scoping diagram indicating the spatial scale (range) of habitat use at different times in the life cycle of two species of lowland fish: Mountain galaxias (*Galaxias olidus*) and Western Carp Gudgeon (*Hypseleotris klunzingerii*). Note the extended range of galaxiids later in the life cycle, which reflects an up-stream spawning migration and highlights the importance of connectivity for successful recovery of these populations.

that while one species, the carp gudgeon, is likely to respond to localised habitat restoration (pool formation) alone, whereas another, the mountain galaxias, will require not only residential habitats to be restored, but also longitudinal connectivity between adult, spawning and larval habitats for populations to recover. These differences in habitat requirements over the life cycle of each species results in markedly different scope diagrams (Fig. 1), and hence the concept of scope encompasses, and draws attention to, the need for connectivity.

Habitat encompasses a range of variables and augmenting physical habitat can clearly be guided by an understanding of the nature of the habitat template. However, such a strong focus on habitat restoration draws on the assumptions that if habitat is restored, the threatened species will return or their populations recover (Palmer, Ambrose & Poff, 1997), and it is this myth that has unwittingly underpinned stream restoration (Hilderbrand *et al.*, 2005). Fortunately, as regards stream fish, it has now been realised that to understand fish population dynamics, the parts of the stream system occupied over the life cycle of the target species needs to be known (Schlosser, 1991; Fausch *et al.*, 2002). Consequently, efforts at habitat restoration for fish have begun to incorporate habitat requirements throughout the life history (Imhof, Fitzgibbon & Annable, 1996), including both the ontogeny of habitat use and dispersal.

Disturbance and refugia

Natural streams are subject to hydrological disturbances in the form of floods and droughts. Floods are mostly pulses whereas droughts are ramps, i.e. disturbances that steadily increase in strength and extent (Lake, 2000). A critical habitat requirement for population persistence is the availability of refugia from natural disturbances (Sedell *et al.*, 1990; Lancaster & Hildrew, 1993), even if they are only used occasionally. Surviving disturbances may depend on life-history adaptations (e.g. desiccation-resistant eggs, flying adults), but in many instances particular habitats serve as the refugia (Lancaster & Belyea, 1997). The refugia for surviving floods are quite different from those used to survive drought (Boulton, 1989; Brooks, 1997). Refugia may also be needed for other types of disturbance. For example, cold-water refuges generated by groundwater entering the channel allow cool-water fish, such as salmonids, to deal with high summer water temperatures (Ebersole, Liss & Frissell, 2003). In many degraded situations not only have residential habitats been reduced or lost, but so have the required refugia (Bond & Lake, 2005a,b). Thus, for particular species, residential habitat requirements must be restored along with the adequate provision of suitable refugia capable of enhancing the resistance and resilience to both natural and anthropogenic disturbances (Bond & Lake, 2005a). For example, channelisation increases the severity of floods directly, but also reduces the availability of flow refugia, leading to a reduced capacity of biota to recover from floods (Negishi, Inoue & Nunokawa, 2002). There are few examples from the literature in which refugia from disturbance have been actively targeted in restoration, although constructed habitats have been used to provide a refuge or 'sanctuary' from surrounding human disturbances (Winemiller & Anderson, 1997).

Connectivity and fragmentation

The issue of dispersal extends beyond the linking of habitats used at different life stages, and is vital to the persistence of metapopulations at the landscape scale (Hanski & Gilpin, 1997; Downes & Keough, 1998). Restoring population viability may, in many cases, involve adjusting links between various sub-populations, which may have originally been part of

a metapopulation, and which may now only be isolated remnants. The hierarchical, unidirectional structure of stream systems, especially as regards the low-order streams, means that dispersal between isolated populations is considerably more difficult than between populations living in multidirectional systems (Fagan, 2002; Lowe, 2002). Dispersal for fully aquatic species between adjoining sub-catchments may be difficult, involving travel over considerable distances (Fagan, 2002), and thus may be limited (Hughes *et al.*, 1996). Even for insect species with winged adults, dispersal within catchments may be very limited (Wishart & Hughes, 2003; Briers *et al.*, 2004). Thus, the loss of connectivity (i.e. fragmentation) may be particularly severe, and recovery may be slow, even in the absence of artificial barriers to movement. In the case of native galaxiid fish in south-east Australia and New Zealand, populations once confluent across several stream orders are now isolated relict populations confined to low-order headwater streams. This confinement has been created by the introduction of trout (Fletcher, 1986; Crowl, Townsend & McIntosh, 1992), with natural barriers such as waterfalls, preventing trout from reaching the isolated populations. In some cases it has been possible to restore galaxiid populations (such as *Galaxias fuscus* Mack.) via the removal of alien trout and the creation of new downstream barriers to prevent trout from reinvading upstream stream sections (Lintermans, 2000; Lintermans & Raadik, 2003). In general, the success of this approach relies on the presence of appropriate habitat conditions within headwater reaches and assumes that migratory and inter-population movements of the native target species will not be negatively affected (Novinger & Rahel, 2003).

As streams become larger, the dispersal framework becomes more linear rather than dendritic. Thus, if there are no barriers, species in large rivers may have extensive linear dispersal along the main channel, but dispersal between channel and floodplain wetlands may be curtailed through human floodplain development and flow regulation (Ward & Stanford, 1995; Ward *et al.*, 2001). Whether dealing with ontogenetic habitat shifts or population dynamics that incorporate elements of metapopulation theory, an improved understanding of dispersal patterns, both in natural and fragmented stream systems, will greatly enhance our ability to restore populations.

In landscape ecology a key concept is connectivity, the degree to which the landscape facilitates or impedes movement among resource patches (Taylor *et al.*, 1993). In the literature the movement usually relates to organisms and their propagules rather than the movements of energy and nutrients (Turner, Gardener & O'Neill, 2001). Connectivity has been divided into two related types: structural connectivity, the pattern of structural connectedness between landscape elements, and functional connectivity, which refers the degree to which 'the landscape facilitates or impedes movement among resource patches' (Bélisle, 2005). For many organisms the levels and patterns of connectivity between resource patches is critical and loss of connectivity by various means, human or otherwise, increases the degree of fragmentation. Greater fragmentation increases the risk of local species extinction, biodiversity loss (Fagan, 2002; Fahrig, 2003) and possibly the weakening of processes, such as the movement of nutrients. Landscape restoration often seeks to restore connectivity through the installation of corridors between isolated patches (Turner *et al.*, 2001).

In stream ecosystems the axes of connectivity – longitudinal, lateral and vertical – are critical to both ecosystem structure and function (Ward, 1989). The functional dependency of longitudinal connectivity (espoused in the River Continuum Concept; Vannote *et al.*, 1980) in stream ecosystems and the breaking or reduction in the strength of barriers is key to many restoration projects. Linked with connectivity there has been a steady realisation of the overriding importance of the natural flow regime in determining patterns of connectivity and community dynamics (Poff *et al.*, 1997), in a large part because of flows needed for lateral connectivity to floodplains.

Dams disrupt both longitudinal and lateral connectivity. Besides being barriers, dams with accompanying river regulation change flow regimes and by creating lentic reservoirs cause major changes in sediment, nutrient and organic matter dynamics and transport. As dams age, uses may alter and with public attitudes changing, dam removal is increasingly becoming a restoration strategy (Doyle *et al.*, 2003). If the removal of small dams is carefully managed, it is quite possible to greatly reduce the harmful effects of nutrient and sediment release and to restore both habitat and connectivity (Hart *et al.*, 2002; Stanley & Doyle, 2003). Studies on small dam

removal may generate knowledge for undertaking the removal of large dams. Threats to successful restoration from exotic species may require the introduction of barriers to segregate and protect native species thereby reducing longitudinal connectivity.

Lateral connectivity, that emphasizes channel-floodplain connections as conceptualised in the Flood Pulse Concept (Junk, Bayley & Sparks, 1989), is often considered in projects emphasising restoration of environmental flows. In many cases, however, the concentration of effort is almost solely on the provisions of flow rather than consideration of the spatial specificity and timing of floodplain ecological processes (Robertson, Bacon & Heagney, 2001), and the interactions between these processes and land use practices on floodplains. In southern Australia the dominant floodplain tree (*Eucalyptus camaldulensis* Dehnh.) recruits by the stimulation of seed germination after floods (Bren, 1993); however, recruitment has not only been limited by the reduction in floods because of river regulation, but also by cattle grazing on the floodplain, which reduces the groundcover and increases seed predation by ants (Meeson, Robertson & Jansen, 2002). Whilst water may be released from reservoirs to augment stream flow, the fact that the downstream delivery of sediment, nutrients and organic matter is greatly reduced by processes operating within the reservoir, has been rarely considered in restoration projects. The seasonal linking of processes on floodplains may not be considered in providing environmental flows as floods on the floodplain, so that both timing and duration of such floods may be quite aberrant.

Restoration by revegetating riparian zones also enhances lateral connectivity, but further influences physical, chemical and biological processes such as bank stabilisation, shading, and regulation of sediment and nutrient inputs, all of which are mediated by the terrestrial-riparian ecotone (Naiman & Décamps, 1997; Ewel *et al.*, 2001). In relation to the riparian zone functions, it is clear that width is important to allow the effective interception of nutrients and sediments (Lowrance, 1998) and that fragmentation of riparian zones, even by small gaps, may impair these functions (England & Rosemond, 2004). Several studies (Storey & Cowley, 1997; Scarsbrook & Halliday, 1999) have shown that the lengths of forested riparian zone determine the effectiveness of

restoration of stream structure and function. In the transition from open pasture to native forested riparian zone in New Zealand, Storey & Cowley (1997) found that temperature and oxygen levels in the stream recovered within 300 m, while the fauna recovered over 600 m and chemical processes were variable and only partly recovered over 600 m.

In the channels of natural streams, pieces of large wood create habitat for biota as well as serve to increase the retentive capacity of the channel (Tabacchi *et al.*, 1998; Gregory, Boyer & Gurnell, 2003). Coarse wood in streams provides habitat surfaces for organisms such as biofilm algae to grazing snails, provides a food resource to specialised invertebrates such as elmids beetles, and creates habitat such as downstream scourpools (Gregory *et al.*, 2003). 'Living wood' in rivers can serve to create islands (Gurnell *et al.*, 2005). Most of this wood, both dead and living, comes from riparian trees. The restoration of native trees in degraded riparian zones may take considerable time before maturity is reached and it may take even longer before dead wood is donated to the stream. In the interim, instream timber may have to be supplemented by additions (e.g. Kail & Hering, 2005)

Vertical connectivity – the links between the hyporheic zone and the stream channel – has rarely been considered in restoration (Meidl & Schönbon, 2004; Hancock & Boulton, 2005). Extensive sediment inputs to streams can clog interstitial sediments (colmatation), disrupting hyporheic exchange, and contaminated groundwater derived from the surrounding catchment may enter the hyporheic zone (Brunke & Gonser, 1997; Boulton, Depauw & Marmonier, 2002; Meidl & Schönbon, 2004). Both of these processes lower dissolved oxygen and elevate nutrient concentrations in the hyporheic zone. Due to vegetation clearing in some catchments, massive erosion has led to high sediment loads being transported downstream and forming sediment slugs in sections of lower stream power. These sediment slugs form a new hyporheic zone that may reduce available carbon and surface water availability and may dramatically change nutrient dynamics, especially those of nitrogen and phosphorus. Restoration to generate and maintain habitat heterogeneity in such sand slugs is very difficult and remains an unresolved challenge (Hancock, Boulton & Raine, 2001; Boulton, in review).

Food web theory

General ecological theory on the trophic structure of communities in ecosystems has historically emphasised the derivation and processing of autochthonous organic matter, even though in stream ecology allochthonous organic matter has long been recognised as a major food source in shaded streams. In recent years, it has increasingly been recognised that subsidies across ecosystem boundaries may be important, if not critical, to maintain an ecosystem's trophic structure (Polis, Anderson & Holt, 1997). The input from terrestrial vegetation to streams of organic matter that ranges from dissolved organic matter, through leaves and other litter to large wood pieces has long been recognised as a critical donation from the riparian zone into streams (Hynes, 1975; Cummins *et al.*, 1984). This subsidy is critical to the functioning of upland wooded streams and it is surprising to find that detritus inputs have rarely been considered in restoration (but see Muotka & Laasonen, 2002). Lack of such inputs can alter shredder densities and production and thus change the trophic structure of stream communities (Hall, Wallace & Eggert, 2000; Eggert & Wallace, 2003). Besides the subsidy of plant detritus, the input of fauna, notably arthropods, may be critical for stream fauna, especially top predators, and loss of this input can initiate trophic cascades (Nakano, Miyasaka & Kuhara, 1999; Kawaguchi, Taniguchi & Nakano, 2003).

There also exists a largely neglected, yet possibly critical, subsidy from the river to the surrounding hinterland, which again can take several forms. For example, riparian zone predators, such as birds (Gray, 1993; Nakano & Murakami, 2001) and spiders (Baxter *et al.*, 2004), may strongly depend on adult insects from rivers for food. When a river inundates its floodplain, there is a boom in aquatic primary and secondary production, much of which may be donated to the surrounding hinterland boosting terrestrial production (Molles *et al.*, 1998; Ellis, Crawford & Molles, 2001; Ballinger, Mac Nally & Lake, 2005). As floodwaters recede across the floodplain, there may be an influx of both carabid beetles and spiders preying on stranded aquatic fauna (Ballinger *et al.*, 2005). These subsidies from aquatic production may greatly benefit the biota of the hinterland, yet they remain largely unrecognised in restoration projects. The fostering of both unidirectional and

reciprocal subsidies (Nakano & Murakami, 2001) may be crucial for the effective restoration of both the terrestrial and aquatic communities of streams and riparian zones.

The importance of top-down and bottom-up processes are widely acknowledged in freshwater food webs (Carpenter, Kitchell & Hodgson, 1985; Power, 1990; Brett & Goldman, 1997). In streams the presence of predatory fish can substantially alter the density of algal consumers and subsequently push the system towards autotrophy and create a trophic cascade (Huryn, 1998; Biggs *et al.*, 2000). Conversely, the exclusion of leaf litter from a detritus-based food web can be detrimental to a vertebrate predator by reducing prey availability – an example of bottom-up control of food web structure in a stream (Johnson & Wallace, 2005). These examples represent cases in which the density or impact of consumers or predators are altered indirectly by changes occurring at other trophic levels. Human-induced disturbances, such as riparian clearing, nutrient enrichment or the introduction of non-native species all have the ability to change food web structure and thus modify community composition. As such, a good understanding of the relative roles of predators and the supply of resources in structuring stream food webs is likely to improve the chances of a successful restoration in circumstances where a community (in its degraded *or* unimpacted state) is governed by strong bottom-up or top-down processes. It is well known, from lakes that increasing predation pressure on planktivorous fish by stocking with piscivores can stimulate profound changes in ecosystem structure and function, a fact that has been used commonly as a restoration tool (Meijer *et al.*, 1999). In streams, while the need to provide food resources has been an implicit component of many interventions, for example riparian revegetation, explicit manipulations of food web structure, either as a tool or a goal have rarely been considered.

Evidence for the importance of supplying basal food resources comes from experiments depriving shaded upland streams of litter inputs, in which there was a loss of shredders and a lowering of decomposition rates (Eggert & Wallace, 2003). Conversely, if forested streams lose their riparian canopy, they become more autotrophic with high primary production and a marked increase in the abundance of scrapers (Wallace & Gurtz, 1986). As forests and

riparian zones develop, primary production and scraper abundance steadily decline and shredder abundances increase (Stone & Wallace, 1998). After clear-cut logging, Stone & Wallace (1998) observed slow and steady declines in primary production and scraper abundance as forests regenerated, with the reverse pattern observed for shredders. This study illustrates the importance that directed changes in energy sources can have in achieving effective stream restoration.

Assembly rules

It is held that communities develop following assembly rules. Unfortunately, the very term ‘assembly rules’ has many meanings and definitions, which creates a problem of effective communication (Belyea & Lancaster, 1999; Booth & Larson, 1999). In this paper we regard assembly rules, following Drake (1990) and Belyea & Lancaster (1999), as rules governing the assembling of communities given dispersal constraints and environmental constraints. Thus, if species from a regional species pool can disperse to a site (i.e. overcome dispersal constraints) and if the environmental conditions at the site allow survival (i.e. the species tolerates environmental constraints) then the assembly rules defined by

internal dynamics – such as interspecific interactions – determine the assemblage structure (Fig. 2a). Assembly rules are concerned with the shaping of assemblage membership and not the environmental constraints.

Species colonising a local site are drawn from the regional species pool (Cornell & Lawton, 1992). This presupposes that the regional pool contains species with appropriate dispersal capabilities and environmental tolerances to inhabit the site (Poff, 1997) and thus, some of its species enter the local pool (Belyea & Lancaster, 1999). This colonisation process from an intact regional pool, which involves dispersal and environmental filters, may apply in many situations. However, in heavily impacted systems the regional species pool may be greatly diminished, and only consist of opportunistic, highly tolerant, generalists (Fig. 2b). Thus, in many situations, such as in urban and degraded rural landscapes, restoration to an historical natural state may be impossible and restoration to any target may be unpredictable without knowledge of the species in the regional pool.

Assembly rules may strongly influence the pathways of succession and presumably restoration. In terrestrial systems, assembly rules have been a strong influence guiding restoration (Lockwood, 1997; Prach *et al.*, 2001), and they have been advocated as guide-

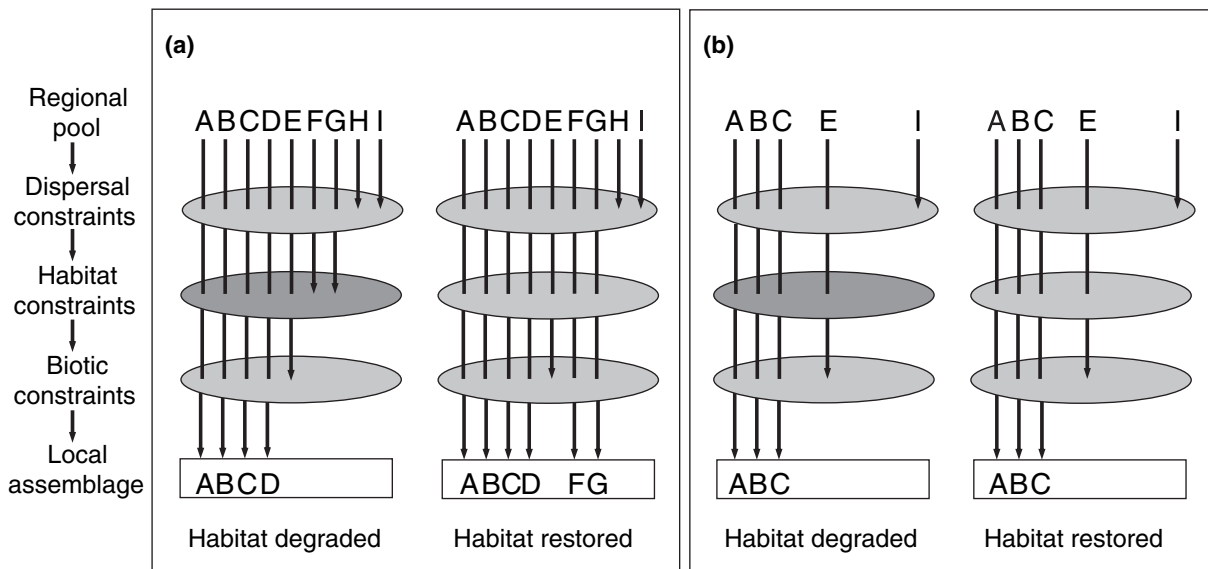


Fig. 2 Hypothetical outcomes of habitat restoration on a local species assemblage with (a) intact and (b) depleted regional species pools. Restoring habitat when the regional species pool is intact allows species F and G to pass through the environment-constraint filter and thus contribute to the local assemblage. However, when the species pool is depleted, comprising only resistant species, restoring habitat does not result in species additions at the local scale (adapted from Rahel 2002).

lines for wetland restoration (Keddy, 1999). As flow-generated disturbance is a major force structuring stream communities, Matthaei *et al.* (2004) suggest that assembly rules involving biotic interactions may be less important in streams than in other ecosystems, and that disturbance in itself may be one of the assembly rules operating in streams. While assembly rules have not been explicitly invoked in stream restoration, it is possible to envision activities within a restoration project as acting, to all intents and purposes, as an assembly rule. This could be performed by generating environmental conditions that influence biotic interactions, thereby favouring the establishment and persistence of species that have particular traits, including tolerances to expected environmental conditions. For example, in the western United States, Rood *et al.* (2005) demonstrated that by reinstating a natural hydrologic regime, the recruitment and establishment of native riparian species, such as cottonwoods (*Populus* spp.) and willows (*Salix* spp.) was favoured over *Tamarix* spp. and other exotic competitors.

Succession, targets and endpoints

Development of communities by succession may follow either of two basic models proposed by Egler (1954). The initial floristic model proposes that after a disturbance, communities develop from the survivors of the original species in the intact community, whereas the relay floristic model proposes that the post-disturbance community develops by colonising species coming in from elsewhere. Both models of succession, especially the relay floristic model encompasses the interspecific interaction of facilitation (Connell & Slatyer, 1977), in which early colonisers modify the environment favourably for later arrivals. For example, in summer with base flow in a sandbed stream, O'Connor (1993) showed that the retreats of net-spinning hydropsychid larvae generated patches that were selectively colonised by baetid nymphs. In stream restoration, facilitation is undoubtedly important as exemplified by macroinvertebrate recovery in Finnish streams, that was found to be dependent on the growth of slow-growing aquatic mosses, not because they provided a food resource, but because they provided habitat structure (Muotka & Laasonen, 2002).

Linked with interspecific facilitation is the concept of ecological engineers – species whose normal activ-

ities create structures that in turn may benefit the activities of others (Jones, Lawton & Shachak, 1997). Clearly in restoration it could be very worthwhile to augment key species that are ecological engineers. Instructive examples include the reintroduction of beavers that has had a major effect on streams and surrounding land, creating conditions for lentic species and altering trophic structure (Naiman, Johnston & Kelley, 1988; Wright, Jones & Flecker, 2002). Even at the small scale, ecosystem engineers may thus be critical to community development.

In newly formed natural streams, such as those formed by receding glaciers (Milner *et al.*, 2000) or in streams devastated by disasters, such as those near Mount St. Helens (Cushing & Smith, 1982; Ward *et al.*, 1983), development of full community structure and ecosystem function may be slow (years) to very slow (decades). In such cases there is primary succession with recognised stages, possibly fitting Egler's relay floristics model (Fisher, 1990).

In many natural streams with marked disturbance regimes, such as desert streams, there is a clear succession in depleted patches after disturbance (Fisher, 1990). In restored (Gore & Milner, 1990) or newly constructed streams (Williams & Hynes, 1977; Malmqvist *et al.*, 1991) close to a natural source of colonists, colonisation and full community development may be rapid (90–400 days; Gore & Milner, 1990). These examples fit the initial floristics model of succession (Fisher, 1990) and the 'rubber band' model of community recovery (Sarr, 2002). That is, if the disturbance is stopped and the habitat rebuilt, then recovery will be complete and may be relatively rapid (Fig. 3a). However, for a variety of causes, such as different dispersal capabilities, priority effects, and the playing out of interactions, it may take considerable time to fully restore a community to the targeted state. Thus, the restoration pathway may be one of hysteresis or follow Sarr (2002) 'broken leg' model, in which the community follows a lengthy and non-linear trajectory to recovery (Fig. 3b).

Because of restricted dispersal from intact sources (perhaps exacerbated by the dendritic geometry of streams; Fagan, 2002), community restoration may be slow and incomplete (Fuchs & Statzner, 1990; Bond & Lake, 2003b) – making subsequent restoration akin to Egler's (1954) relay floristics model – where most of the species have to colonise from afar (Fisher, 1990). This may mean that as different colonists

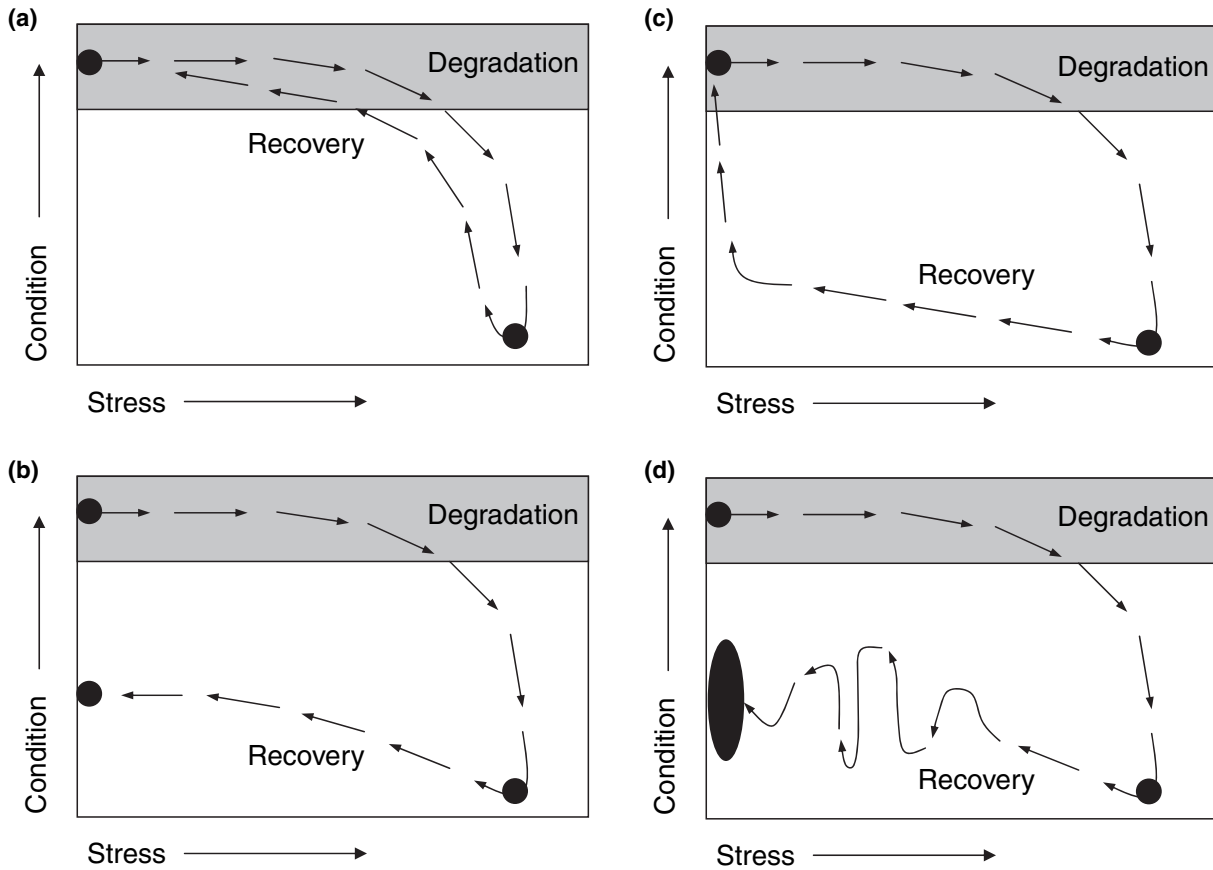


Fig. 3 Four potential degradation-recovery pathways (adapted from Sarr, 2002): (a) the ‘rubber band’ model in which recovery follows closely the pathway of degradation, (b) the ‘hysteresis’ model in which recovery follows a lengthy, non-linear pathway as stress is removed, (c) the ‘Humpty–Dumpty’ model in which recovery could follow various trajectories but the endpoint is distinct from the predegraded condition and (d) the ‘shifting target model’, an extension of the ‘Humpty–Dumpty’ model in which the recovery pathway itself is unpredictable and the endpoint becomes a shifting target bounded by distinct limits (hatched area). Condition on the y-axis corresponds to any indicators adopted as targets within the restoration project.

arrive at different times, the new community may be quite different in terms of species composition, even when species richness is equivalent to reference targets. This ‘Humpty–Dumpty’ effect model (Pimm, 1991; Lockwood & Pimm, 1999) could mean that ‘restored’ assemblages are structured along a variety of paths (Fig. 3c; Hobbs & Norton, 1996). Restoration of this type may arrive at a stable endpoint, but, because of forces, such as disturbance causing changes in species membership and resource levels, the assemblage undergoing restoration may not follow a predictable trajectory (Fig. 3d). Without stability the endpoint becomes itself a shifting target that may be bounded by distinct limits. For example, in perennial (Lake, Morton & Milne, 1988; Hildrew & Giller, 1994) and temporary streams, both temperate (Boulton & Lake, 1992) and tropical (Douglas, 1999),

there are predictable seasonal changes in the composition of macroinvertebrates irrespective of the disturbance regime. This pattern suggests that short-lived stream biota follow trajectories determined by a strong attractor that is driven by predictable changes in seasonal conditions. In degraded streams, such as those exposed to strong press disturbances (e.g. organic or heavy metal pollution; Hynes, 1960; Norris, Lake & Swain, 1982), the greatly reduced fauna appears to be constant irrespective of season. Thus, the trajectory of restoration may be one in which variability is increased, and finally results in oscillations around a strong seasonal attractor. Whereas the restoration of terrestrial vegetation has been analysed in this way (Anand & Desrochers, 2004), this does not appear to be the case for stream ecosystems.

An additional factor potentially affecting trajectories of recovery in many restoration projects is the impact of invasive species, which may act to subvert expected succession pathways. For example, in southern Australia, succession of riparian vegetation may be blocked by fast-growing invaders, such as blackberries (*Rubus* spp.) and Reed Sweetgrass [*Glyceria maxima* (Hartm.) Holmb.], the latter of which may act as an ecosystem engineer by creating major changes in sedimentation in addition to nutrient dynamics (Clarke, Lake & O'Dowd, 2004). In south-western U.S.A., saltcedar (*Tamarix ramosissima* Ledeb) is an active invader that reduces native riparian cover (Busch & Smith, 1995) and thus alters stream ecosystem processes such as organic matter breakdown (Kennedy & Hobbie, 2004). Similarly, 'swampers' (space monopolisers) such as the New Zealand mud snail (*Potamopyrgus antipodarum* Gray; Schreiber, Quinn & Lake, 2003) or the zebra mussel (*Dreissena polymorpha* Pallas; Strayer *et al.*, 1999) may result in a benthic community in 'restored' streams being very different from that made up of the original native species. The impact of invasive species on restoration need not be a passive one. For example, up until quite recently in Australia, with the aim of 'restoring' riparian zones, non-native willows (*Salix* sp.) were actively planted within riparian zones, with a variety of detrimental impacts on riparian and instream ecosystem processes (Read & Barmuta, 1999; Greenwood, O'Dowd & Lake, 2004).

Finally, in a growing number of ecosystems, alternative states, largely under endogenous controls and bounded by critical thresholds, are being detected (Carpenter, 2001). Such states have been targeted for restoration, such as the clear water, macrophyte-dominated state in shallow eutrophic lakes (Scheffer *et al.*, 1993). However, in most streams seasonal periodicity is very marked: resistance in response to natural disturbances is relatively low but resilience is high (Fisher & Grimm, 1991; Lake, 2000), resulting in continuous changes in species abundance and composition. Such dominance of community structure by exogenous physical factors, generated by flow and substrate, may preclude the development of alternative stable states maintained by internal dynamics and delineated by clear critical thresholds, even though they have been suggested to occur in streams (Dent, Cumming & Carpenter, 2002).

Ecological processes and species richness

In stream restoration in particular, and restoration in general, the implicit assumption is made that with the recovery of species and their resources, ecological processes will also be restored. With restoring habitat, the expectation is that the species will return (the 'Field of Dreams' hypothesis; Palmer *et al.*, 1997), and in recovering diversity, the expectation is that the ecological processes will be re-established. Such an assumption rests upon the somewhat controversial tenet that ecosystem functioning is related to biodiversity (Hooper *et al.*, 2005). This issue arose through concern about how species loss in an ecosystem could affect ecosystem functioning (Lawton, 1994), and much of the ensuing debate in this area has centred on the issue of species loss, and the various hypotheses of how ecosystem functioning would respond. Such hypotheses include those of 'rivet-popping' (Ehrlich & Ehrlich, 1981), redundancy (Walker, 1992) and idiosyncratic (Naeem, 1998) ecosystem responses to species loss. Much of the investigation of the biodiversity–ecosystem functioning relationship has been carried out in controlled laboratory and horticultural settings, and it is only recently that field-based experiments have been urged (Giller *et al.*, 2004) and undertaken (O'Connor & Crowe, 2005). In terms of restoration, the critical question is whether increasing species richness increases ecosystem functioning, and whether there are particular species which are more critical to restoring particular aspects of ecosystem functioning than others?

To what extent redundancy in ecosystem functioning exists in stream ecosystems remains much less well known than in terrestrial systems (Covich *et al.*, 2004). For the shredding of coarse particulate organic matter by macroinvertebrates, some evidence suggests that the effectiveness of this functional group is increased with the addition of further species (Jonsson & Malmqvist, 2003b), whereas the litter processing by fungal decomposers is unaffected by changes in species diversity (Dang, Chauvet & Gessner, 2005). For grazers and predators, Jonsson & Malmqvist (2003a) found that species identity was very important in determining process rates, which in a restoration context means that not all species in a functional group are equal and some are much more important than others. Cardinale, Palmer & Collins (2002) found

that increasing species richness of filter-feeding trichopterans in experimental stream channels increased the effectiveness of resource capture and that this effectiveness was maintained by disturbance (Cardinale & Palmer, 2002). These findings suggest that there is limited redundancy in streams for some ecosystem functions, such as leaf-shredding and particle removal by filter-feeding, but not other functions. In terms of restoration this may mean that the full complement of species originally present within particular functional groups may be required to restore particular ecosystem processes.

Scale, hierarchy and disturbance

Undeniably, issues of scale such as grain, extent and context will have an influential effect on the patterns of response and trajectories of change following ecosystem restoration. As pointed out early on by Hynes (1975) and Likens *et al.* (1977), the catchment has an overriding influence on the ecology of the stream, and hence in many cases considerable restoration work on the catchment, such as revegetation, may be required to improve the likelihood of effective stream restoration (Bohn & Kershner, 2002). Unfortunately, the spatial and temporal scales of most restoration activities appear to be set more by logistic, economic and social constraints than by a specific understanding of the scales relevant to specific processes occurring in ecosystems (Lake, 2001). Consequently, much restoration appears to occur at relatively small scales, resulting in fragmented patches of restored habitat embedded in a landscape in which external and large-scale processes (often degradation) continue to dominate over the internal dynamics of restored areas (Beschta *et al.*, 1995; Bohn & Kershner, 2002; Bond & Lake, 2003b).

Understanding how scale influences the linkages between organisms and processes and their environment is a formidable challenge that influences all aspects of aquatic research, including ecosystem restoration (Wiens, 1989; Poole, 2002; Wiens, 2002). The concept of scope is one way by which to tackle the scaling problem (Schneider, 1994; MacNally, 1999). The hierarchical evaluation system for fish habitat proposed by Imhof *et al.* (1996) provides a good example in which the extent of habitat use over the life history of salmonids is incorporated into restoration planning. In general, while scope will vary

widely among different organisms and processes, restoration that encompasses the maximum extent and minimum grain of environmental heterogeneity will probably be most successful. On this basis restoration may only succeed when conducted at large scales (taking into account the large scope of restoration targets), begging the question as to whether restoration of systems, such as large rivers, will ever be successful given that most degrading processes will continue at large scales (Gore & Shields, 1995).

Given this constraint on restoration, two key questions emerge. One question is how ecological processes and population and community dynamics within restored patches change as the size of the restored patch increases? In order to restore the attributes, such as lowered stream temperatures, improved water quality and reduced sediment loads by restoring riparian zones, restoration may need to be carried out at a large scale. In New Zealand, a study of riparian zones of varying dimensions revealed that restoration at isolated sites is compromised if upstream riparian zones are degraded, that long lengths of replanting are required to restore streams, in terms of water temperature and quality, and macroinvertebrates, and that changes in these variables associated with replanting may occur only over long-time spans (Parkyn *et al.*, 2003). Allen & Starr (1982) pointed out that as spatial scale increases, so does the temporal scale of phenomena operating at that scale. This carries with it the difficult problem that to effectively monitor large-scale restoration there is the need to commit to a long time span. Restoration at the local scale may proceed much more rapidly than that at the large scale, as illustrated by the times for recovery of small- to large-stream patches (Gore & Milner, 1990).

The second question is how large-scale disturbances affect restoration at the local 'site' level? Not only can small-scale restoration be overwhelmed by large-scale influences (Beschta *et al.*, 1995; Bohn & Kershner, 2002; Bond & Lake, 2003b; Pretty *et al.*, 2003), but large-scale disturbances, such as floods and drought, may destroy small-scale efforts, thereby necessitating continued interventions to achieve any form of success. It has been argued that small-scale restoration can only be undertaken if large-scale disturbances at the catchment scale have been removed or greatly reduced (Beschta *et al.*, 1995; Bohn & Kershner, 2002).

However, given that restoration at the catchment scale will be usually infeasible, the challenge lies in determining where within the catchment, site-specific restoration activities should be undertaken to reduce the impacts associated with large-scale degrading processes.

As an example, if a functioning metapopulation can be established by facilitating dispersal amongst restored habitat patches distributed across the catchment, long-term population persistence at the landscape scale may occur even though much of the landscape remains degraded. There are few studies addressing this issue directly, but those by Labbe & Fausch (2000) and Fagan (2002) on desert fishes demonstrate the importance of interpatch dynamics in facilitating population persistence. Likewise, upstream restoration, such as re-establishment of riparian vegetation, may improve downstream conditions and increase the effectiveness of downstream restoration. Improvements in functional connectivity and water quality and decreases in sediment and nutrient loads are feasible outcomes of such restoration.

An important consideration in restoration is to achieve a restored state that persists through the prevailing disturbance regime (Westman, 1991). This may be difficult as in many situations the original and natural disturbance regime has been replaced by a very different and usually more severe disturbance regime. For example, excessive sedimentation in stream channels may exacerbate the effects of low flow and drought when streams cease to have surface flow and loose pool refugia (Bond & Lake, 2005). However, it may be impossible to restore streams to the state in which they are resilient to large-scale ramp disturbances, such as catchment salinisation (Hart *et al.*, 2003) and long-term changes in flow and increased frequency of extreme events resulting from global climate change (Pittock, 2003).

Conclusions

In current stream restoration efforts, there may be an awareness of principles established in stream ecology. These include the crucial importance of connectivity, of having sufficient flows, of the need for effective energy and nutrient processing, of providing appropriate habitat, and of natural and anthropogenic disturbances. However, it is rare to see such ideas

specifically mentioned in stream restoration work. This lack of recognition may reflect the lack of ecologists involved in restoration projects, the fear by practitioners that experimentation and monitoring may disrupt the project, or the lack of sufficient benchmarks and insufficient knowledge on the ecology of natural rivers, especially floodplain rivers (Ward *et al.*, 2001).

It is clear that stream restoration projects may, in turn, be very useful in furthering our understanding of basic ecology by allowing the testing of ideas on population dynamics, of community assembly and persistence, and of ecosystem structure and function. The larger the spatial scale and the longer the duration of the project, the more valuable restoration becomes in evaluating long-term dynamics, and in providing a framework for embedding small, well-designed projects that test particular mechanisms and interactions. In using or testing ecological theory in restoration, clear goals and possibly trajectories should be set, and the course of the restoration effort adequately monitored. This presupposes that there is careful planning at the beginning of projects, that informed selection is made of indicators, that ideally provisions are made for gathering pre-restoration data, and that there is a rigorous design for monitoring.

In the planning stage, it is essential that there are inputs from a range of relevant disciplines (e.g. hydrology, geomorphology, biogeochemistry, statistics) and interests (resource management, economics, local stakeholders). At this stage an assessment should be made of the feasibility of the restoration intervention. Does the scale of the intervention match the scope(s) of the target organisms and/or ecological processes? What are the constraints (apart from funding and resources) upon the project? In dealing with constraints one is usually dealing with disturbances, which are usually many and interactive and may include legacies of disturbances past. It must also be borne in mind that in restoration, one is hoping to attain goals that not only fit into the local prevailing disturbance regime, but may also fit into large-scale anthropogenic disturbances, such as land use change and global climate change.

Concepts from landscape ecology are now starting to be applied to streams (e.g. Townsend, 1989; Poole, 2002; Wiens, 2002) and this may create new ways of looking at streams involving such concepts as hierarchical patch dynamics (Poole, 2002). It may also allow

the refinement of concepts integrating catchment and stream biota and processes. Such new directions should provide valuable insights and concepts to advance the restoration ecology of streams.

We have attempted to provide a broad cross section of ideas drawn from ecological theory that may be of importance to the restoration of stream ecosystems. Many of these do not arise directly from the freshwater literature, yet many have the potential to inform or guide thinking in the area of stream restoration. The selection of ideas is by no means exhaustive, nor should they be seen as mutually exclusive. Indeed, in most instances it will be necessary to incorporate many aspects of ecological theory if we are to truly restore ecosystems. It is perhaps also true that many of the ideas we have addressed are often unknowingly incorporated into restoration projects, although more often as assumptions rather than as explicit hypotheses. As such, many of these ideas continue to go untested within the context of restoration. Only by improving the links between restoration activities and ecological theory will we develop our understanding of the way in which ecosystems function, and hence the means by which they may be restored in the long term.

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