MINI-REVIEW

Habitat analogues for reconciliation ecology in urban and industrial environments

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Summary

1. Current views of anthropogenic environments emphasize the extreme novelty of urban and industrial ecosystems. Proponents of reconciliation ecology argue that we need to use such habitats to conserve biodiversity, given the inadequacy of natural reserve systems.

2. Some of the harshest anthropogenic ecosystems may be able to support indigenous biodiversity due to their structural or functional resemblance to natural ecosystems, habitats, or microsites that may be present in the region but not part of the historic ecosystem on a particular site. Here we review recent work that evaluates similarities between urban and industrial ecosystems and natural analogues, and explore the potential for these in reconciliation ecology.

3. We find that artificial habitats represent a gradient of ecological novelty which may be independent of the degree of human influence. While hard-surfaced habitats such as walls and quarries are the most investigated artificial analogues (of natural rock pavements and cliffs), there are many other examples spanning a range of habitats in both terrestrial and marine settings. Analogous ecosystems may be present in the region but limits to dispersal can prevent appropriate species from reaching urban or industrial sites, and small differences in abiotic conditions can sometimes prevent colonization by native biota in otherwise similar artificial habitats. We suggest that a search for habitat analogues represents an important principle to guide reconciliation ecology in urban and industrial lands. In constrast, analogous ecosystems may also support pest species that exploit the similarities between anthropogenic habitats and their ancestral habitats.

4. *Synthesis and applications*. Identifying analogous habitats and ecosystems could enhance biodiversity conservation and ecosystem services in anthropogenic environments. Abiotic and biotic differences between artificial analogues and natural systems can be frequently overcome by ecological engineering to make the environment more suitable for native biodiversity, and/or assisted dispersal to allow suitable native organisms to reach appropriate sites within artificial ecosystems. Altering some habitats to become less analogous may help reduce impacts of pest species in urban and industrial areas.

Key-words: disturbance, ecological engineering, hardscape, no-analogue state, restoration ecology, rock outcrop, stress

Introduction

Ecological comparisons between urban or industrial environments and natural areas emphasize their differences. In the prevailing view of anthropogenic ecosystems, they cause stress for many native organisms because they differ substantially from the natural habitats they replaced: new combinations of environmental conditions and organisms represent a 'no-analogue future' (Hobbs *et al*. 2006; Fox 2007; Seastedt, Hobbs & Suding 2008) and restoring ecosystems to their original condition will be very difficult (Choi 2007). Anthropogenic ecosystems are considered to be ecologically novel in that climatic conditions, soils, toxins, hydrology, productivity, species composition and interactions (Pickett *et al*. 2001) differ from conditions prevailing prior to human alterations. At fine

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spatial scales, habitat patches and microclimates are often altered compared to natural areas, but other processes such as resource addition and climatic change alter processes affecting entire urban ecosystems (Shochat, Warren & Faeth 2006). Urban ecosystems are also framed as novel because human cultural and economic activities strongly influence fundamental processes and structures (Pickett *et al.* 2001; Williams *et al.* 2009).

Post-industrial environments are likewise seen as heavily altered at a variety of spatial scales due to the dramatic nature of extractive or manufacturing processes, featuring removal or addition of biotic and abiotic materials in massive quantities (Bradshaw 1987). The main view is that anthropogenic ecosystems are largely distinct in structure and function from the natural ecosystems they replaced because of alterations to resource availability, stress intensity, disturbance, and changes in the spatial arrangement of ecosystem components (Kozlov & Zvereva 2007). These phenomena are often studied along gradients of human influence, where the greatest degree of ecological novelty (as exemplified by increased disturbance and propagule pressure from non-native species) is associated with the greatest human impact (Fig. 1) (Guntenspergen & Levenson 1997). Natural phenomena such as genetic mutations, long-distance colonization of non-native organisms, and biological interchanges following geological events such as the development of land bridges connecting continents can also create ecological novelty in the absence of human influence (Vermeij 1991). Thus ecological novelty and human influence on ecosystems can be conceptualized as orthogonal gradients, or more simply as four quadrants representing combinations of novel vs. analogous and low vs. high human influence (Fig. 1). Natural remnant habitats may have little evidence of novelty or human influence, but anthropogenic disturbances such as addition of toxins to ecosystems can create novel ecosystems with no natural analogues (Fig. 1), such as PCB-contaminated soils. However, where human activities produce habitats that have natural analogues, such as stone walls that are similar to natural cliffs, habitats strongly influenced by ongoing or historical human activities can be ecologically analogous to natural habitats (Fig. 1).

Recognizing that conservation of native biodiversity within natural area reserves is unlikely to preserve viable populations of the majority of Earth's species, Michael Rosenzweig (2003) has proposed an alternative approach, reconciliation ecology, in which species are conserved in highly altered, anthropogenic habitats in urban or industrial lands. Examining such habitats, ecologists have long recognized a small subset of native species that can exploit highly altered, anthropogenic habitats in urban (McKinney 2002) and industrial (Ratcliffe 1974; Johnson, Putwain & Holliday 1978; Usher 1979) settings. However, the list of native species that have spontaneously colonized these habitats is typically small. Urban and industrial ecosystems in different regions also attract a consistent biota (Ursic, Kenkel & Larson 1997; McKinney 2006; Kirmer *et al.* 2008; Tomlinson *et al.* 2008), and thus can be more similar to each other than to nearby natural habitats. These consistencies

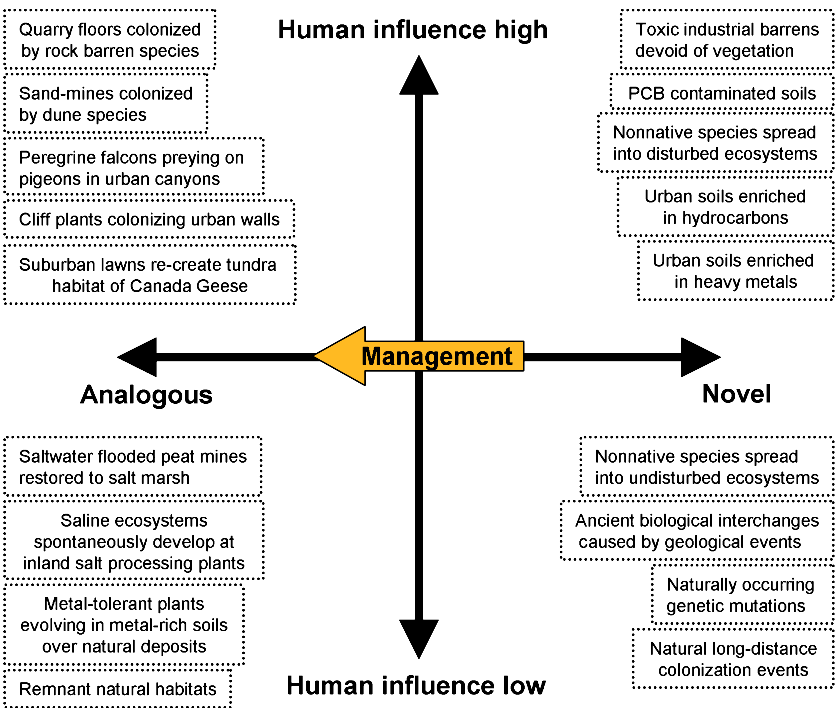

Fig. 1. Conceptual framework showing examples of ecosystem processes or structures along two gradients: a human influence gradient which describes the degree to which active intervention by humans has led to current conditions; an ecological novelty gradient which describes the degree to which the ecosystem is analogous to natural ecosystems. In this framework, active management can take novel situations and make them more analogous to natural ecosystems. We propose that these represent continuous gradients, but placement of the ecosystems/processes mentioned here was limited to the four quadrants; no attempt was made to assign positions within a quadrant.

suggest common ecological features that could provide a more generalizable basis for reconciliation ecology in anthropogenic ecosystems. Here we argue that one productive approach to reconciliation ecology is to first take a closer look at those native species considered to be successful colonizers of urban (McKinney 2002) or post-industrial landscapes (Kozlov & Zvereva 2007) and examine species traits and habitat conditions that promote their success (Rehounková & Prach 2010). Despite the spread of novel ecosystems, mounting evidence suggests that there are consistent and persistent similarities between natural analogues and particular habitats or microenvironments within anthropogenic ecosystems. Here we review examples of urban and industrial habitats, developed over centuries of global change and massive human influence, which are analogous to natural ecosystems and could represent resources for reconciliation ecology. We also review studies which describe interventions that make habitat analogues more abiotically and biotically similar to natural ones to further expand their utility for biodiversity conservation.

Urban ecosystems

The primary approach to describing and classifying abiotic conditions and processes in urban ecosystems has been to compare them with original (pre-disturbance) ecosystems of the region and, as such, reference conditions in much of North America and Europe are various forest ecosystems (Kaye *et al.* 2006). Almost inevitably, such comparisons indicate that urban environments differ vastly from original ecosystems, and impose high stress on the biota originally occupying the landscape (upper right quadrant, Fig. 1). For example, urban soils are characterized by altered hydrology, raised pH, greater nutrient concentration, higher calcium levels, more rocks, greater decomposition rates, less organic matter, and compacted mixtures of anthropogenic materials compared with local natural remnant ecosystems (McDonnell *et al.* 1997; Jim 1998). Hydrology in urban areas is characterized by less infiltration and more runoff than in more soil-rich environments (Pickett *et al.* 2001; Pickett & Cadenasso 2008, 2009).

While ecosystem processes in urban systems are influenced by human engineering and socioeconomics (Kaye *et al.* 2006; Williams *et al.* 2009), many of the above features of urban soils and hydrology can be found in rock-based ecosystems such as cliffs and rock pavements, especially on limestone (Larson, Matthes & Kelly 2000): higher pH is due to calcareous rock; soil compaction, stoniness, and hydrological properties are due to the natural hard surfaces; and nutrient enrichment occurs through cyanobacterial crusts, thus these may represent analogous, not novel ecosystems (upper left quadrant, Fig. 1). On the other hand, these analogous habitat patches are nested within urban ecosystems characterized by highly altered resource flows and disturbance regimes (Kaye *et al.* 2006; Shochat *et al.* 2006), such that they represent analogous habitat patches within novel ecosystems. Despite their overall novelty urban ecosystems can contain patches with abiotic structure similar to natural habitats, and where appropriate native biota may or may not be present (Hobbs, Higgs & Harris 2009). The relevant ecological question is therefore whether the similarities between habitat patches that are obvious to human observers are similar enough to natural analogues to have potential value for native biodiversity.

Hard surfaces or ‘hardscapes’ common to modern cities have long been recognized as analogous to natural rock outcrops, cliffs, and shingle beaches (Fig. 2). Plants that spontaneously colonize urban hard surfaces tend to be drawn from local natural ecosystems dominated by rocks or shallow soils (Woodell 1979; Larson, Matthes and Kelly 2000; Lundholm & Marlin 2006). Insects find the equivalent of cliffs and scree slopes in industrial ecosystems such as quarries and railways (Eversham, Roy & Telfer 1996). Scorpions in urban Rome are typically found under stones or in stone walls, buildings and ruins, with species typically found in limestone bedrock ecosystems predominating in limestone cement basements, while species originating in volcanic habitats prefer basalt rock walls (Crucitti, Malori & Rotella 1998).

Hard-surfaced urban environments represent exactly the kind of high-stress anthropogenic ecosystem described by Hobbs *et al.* (2006) as novel, but rather than representing a completely novel environment only inhabitable by non-native ruderal species, the literature suggests these areas are in fact colonized by stress-tolerant perennials native to natural rock outcrops and capable of long-term persistence within urban hardscapes (Rishbeth 1948; Larson, Matthes and Kelly 2000; Daniel & Lecamp 2004). On the other hand, a study that directly compared natural and artificial rock outcrops (walls) found that, while a handful of rare native species were more abundant on walls than natural outcrops, most natives occurring on walls were generalists and were widespread in many types of habitat (Láníková & Lososová 2009). Walls tend to have high beta-diversity, suggesting a strong influence of surrounding land uses and propagule pressure from these areas (Francis & Hoggart 2009; Láníková & Lososová 2009). Also, the lack of microhabitat heterogeneity is cited as a possible reason for lower diversity on walls compared with natural rock outcrops (Láníková & Lososová 2009), while alterations to the river wall habitat have been proposed in order to improve the habitat for native species (Francis & Hoggart 2008). For native species to colonize artificial substrates, they must be able to arrive at the site and tolerate the conditions on the site. These studies on artificial walls suggest that dispersal limitations may prevent suitable native species from reaching these sites, and there may be microhabitats missing from artificial walls. Thus, while a small number of native species already exist in particular urban habitats; the questions relevant to reconciliation ecology become: to what extent could more species colonize such habitats should propagule limitations be overcome, and can microhabitats be altered to support more native species?

While cities are covered by hard surfaces, many distinct types of ecosystems exist on urban landscapes as islands in a matrix of hard surfaces. Urban ecosystems contain analogues of several different habitats from the perspective of insects (Eversham, Roy & Telfer 1996), and plants adapted to ecosystems including floodplains, dunes, and other non-forested habitats (Wittig 2004). Ecosystems that have developed on inland

Fig. 2. Urban ecosystem analogues. Clockwise from top left: vines colonize urban cliff analogue. Canada geese *Branta canadensis* utilize lawns as tundra feeding grounds. Green roofs offer analogous conditions to rock pavements or grasslands over shallow soil. Spanish moss (*Tillandsia* sp.) colonizes aerial cables as a tree branch analogue. Stone walls provide habitat to bryophytes and vascular plants. Urban grape vines *Vitis riparia* climbing telephone pole. Lichens colonize brick and stone walls. Pigeons/rock doves *Columbia livia* colonize artificial 'rock ledges'.

salt mines and factories, and roadsides treated with salt have attracted assemblages of species typical of salt lakes and marshes, the nearest natural examples of which can be thousands of miles away (Reznicek 1980). These populations are spontaneous and have spread from their endemic habitats to anthropogenic analogues via human transportation networks, other animals, or long-distance seed dispersal. Some of these halophytes are thought to be native to rare inland salt springs (Reznicek 1980), thus human activities have unwittingly expanded the habitat available for native species and decreased the rarity of particular species associations in the region. This phenomenon has direct applications to urban ecosystems, as halophytes can be used to treat saline waste waters in arid zones (Glenn *et al*. 2009). The prevailing view suggests that salted motorways are completely novel environments (Kowarik 1990), but the habitat analogue perspective suggests that halophytes colonizing these areas are not exploiting novelty but rather responding to conditions resembling those under which they evolved.

Colonization of bombed sites in post-World War II London by fireweed *Chamerion angustifolium* (L.) Holub., a boreal forest species that colonizes after fire and other disturbances, has been taken as evidence of the extreme ecological novelty and artificiality of urban ecosystems (Hill, Roy & Thompson 2002). From the plant's perspective, however, we can surmise that it is behaving completely naturally, colonizing disturbed sites functionally similar to its original natural habitat. Similarly, the black redstart *Phoenicurus ochruros* S.G. Gmelin expanded its range into Britain by colonizing extensive rubble fields in bombed urban areas. While habitat for this rare bird declined as damaged sites were redeveloped, a recent trend sees replication of such stony-field refugia on the rooftops of new buildings (Grant 2006). Ecological engineering involving relatively small modifications to the hardscape can thus create habitat for biodiversity conservation, provided such modifications enhance the degree to which anthropogenic habitats mimic natural ones (in this case the cobble beaches favoured by the redstart). This contrasts with current conceptual models of urban ecosystems in which the hardscape environment is attributed little value for biodiversity conservation (Rosenzweig 2003); some of these rooftops now also support rare invertebrates drawn from dry, rocky or sandy natural habitats (Grant 2006). Students of rock barrens would not be surprised as these ecosystems function as natural refuges for many rare taxa (Larson, Matthes and Kelly 2000).

While no systematic surveys have been undertaken, the ability of urban habitats such as building walls to provide habitat for rare plant species is commonly reported from Europe: nine red-listed plant species are found on walls in Zürich (Guggenheim 1992), and 20 on walls in the German province Niedersachen (Brandes 1992). On the other hand, while wall vegetation in the Czech republic contained one critically endangered, seven endangered, and 12 vulnerable species, analogous natural cliff vegetation contained more rare species (Láníková & Lososová 2009). While Brenneisen (2006) reports three red-listed orchids as having colonized a green roof in Switzerland, he emphasizes that dispersal difficulties and environmental differences still result in faunal differences between green roof and level-ground habitats. Nevertheless, in England, green roofs have been spontaneously colonized by many invertebrate species, of which 10% are considered nationally rare [12% of the total species list of spiders for the U.K. can be found on five green or rubble roof sites studied by Kadas (2002)]. These examples indicate that the ecosystem analogue concept has practical applications in biodiversity conservation, and suggest that some natives can overcome dispersal barriers that prevent other species from reaching urban ecosystems, while other natives may require alterations to specific habitats to facilitate their colonization.

Industrial ecosystems

Extraction and processing of mineral aggregates, ores, and fossil fuels often produces desolate environments characterized by coarse, nutrient-poor or chemically polluted substrates, subject to both intense drought and prolonged flooding (Cooke & Johnson 2002; Walker & del Moral 2003; Kozlov & Zvereva 2007). However, some types of industrial sites have analogues in natural ecosystems, suggesting that rehabilitation goals can be met even if restoration to a historical state is never achieved, by using ecosystem analogues as reconstruction targets and industrial sites as habitat for conservation-priority species and community types (Richardson, Lundholm & Larson 2010). As with urban ecosystems, evidence for such analogues comes from industrial sites attracting consistent biota which are locally novel but regionally confined to specific ecosystem types (Tomlinson *et al*. 2008; Tropek *et al*. 2010). To a greater degree than in urban ecosystems, many experiments testing the idea that native species can thrive in post-industrial ecosystems provided that microhabitat conditions are matched and propagules are made available, have already been performed (Ash, Gemmell & Bradshaw 1994; Herath *et al*. 2009).

Sand-gravel pits and hard-rock quarries are characterized by steep-sloped walls and flat bedrock or shallow-substrate floors prone to drought and flooding due to altered hydrology and geomorphology. Extraction proceeding below the water table often produces water bodies within lower-elevation patches of mined sites. Such conditions are stressful and bar colonization by most propagules immigrating from adjacent remnant ecosystems, yet extraction sites are excellent locations for observing highly diverse assemblages typical of distant rocky outcrops and coastal sand dunes, including rare and endemic species (Davis 1976; Rehounková & Prach 2010; Tropek *et al*. 2010).

Calcareous extraction or waste sites host diverse but consistent biota typical of limestone grasslands in the UK (Ratcliffe 1974), and alvar pavements in Ontario (Tomlinson *et al*. 2008). Similarly, limestone quarry floors in the Czech Republic host spider (Tropek & Konvička 2008), butterfly (Beneš, Kepka & Konvička 2003), plant and arthropod (Tropek *et al*. 2010) species characteristic of rare xeric barrens and scrublands, while quarry walls in Ontario were spontaneously colonized by vegetation indistinguishable from natural cliff-face communities (Ursic, Kenkel & Larson 1997). Sand-gravel pits in the Czech Republic recovered spontaneously to grasslands, woodlands, or wetlands depending on local moisture conditions and regional species pools, highlighting the importance of interactions between immigration and environmental heterogeneity in determining community assembly (Rehounková & Prach 2008). Experiments confirm patterns suggested by observational studies; once immigration barriers were artificially overcome, in the UK alkaline waste was successfully colonized by calcareous grassland species (Ash, Gemell & Bradshaw 1994), while old limestone quarry floors in Ontario were colonized by alvar pavement species including the threatened Great Lakes endemic *Iris lacustris* Nutt. (Richardson, Lundholm & Larson 2010).

Metal-contaminated sites have long fascinated ecologists because although highly toxic substrates prevent successful colonization by most species in the region, such sites are nevertheless noted refugia for a rare but consistent biota with adapted tolerance to heavy metals (Johnson, Putwain & Holliday 1978; Cooke & Johnson 2002). Current concern for conserving metal-tolerant plant species brings to light uncommon natural ecosystems where such species evolved, including serpentines, metal outcrops, and soils surrounding weathered mineral deposits (Whiting *et al*. 2004). Metal-tolerance provides a powerful example of the evolutionary life-history context of the ecosystem analogue perspective: whereas some species present on metalliferous anthropogenic sites consist of populations in which metal-tolerance evolved only after similar industrial sites started appearing in the landscape, other species present clearly evolved over thousands or millions of years in analogous naturally metalliferous ecosystems (Whiting *et al*. 2004) (Fig. 2). Fossil fuel extraction and processing sites also function as refugia for native biota. In Germany, flooded lignite mines were spontaneously colonized by rare orchid species following succession to nutrient-poor, lime-rich wetlands resembling ancestral orchid habitats (Esfeld *et al*. 2008). In the UK, a waste site contaminated with pulverized coal ash developed cover by willow scrub and 'spectacular populations of marsh orchids', and while experimental introduction of a broad spectrum of species to a coal-mined site largely failed, notably dry heath and acidic grassland species were successful (Ash, Gemell & Bradshaw 1994).

Peat-mined sites in New Brunswick, Canada, inundated with seawater following coastal flooding could not be rehabilitated using pre-mine site inhabitants, but salt marsh graminoids established readily, suggesting that salt marshes are useful analogues of salinized peatlands (Montemayor *et al.* 2008). In contrast, barrens created by air pollution from non-ferrous metallurgy may provide an example of industrial habitat with no natural analogue (upper right quadrant, Fig. 1); at such sites most vegetation surrounding point sources of sulphur dioxide and other toxic gas emissions have died and failed to regenerate (Kozlov & Zvereva 2007). Unlike mined sites these industrial barrens remain species-poor, sparsely covered, and provide little refuge for consistent biota typical of other ecosystems. However, some populations managing to tolerate these toxic substrates have apparently arisen through local adaptation by regionally common generalist species (Kozlov & Zvereva 2007). This suggests that a major axis determining how biota representative of analogous vs. genuinely novel ecosystems contribute to succession in post-industrial sites is the length of time that selective agents analogous to industrial impacts have existed in the regional landscape. Industrial ecosystems are heavily disturbed relative to historical conditions but may occupy various positions along a novelty continuum, dependent on the extent to which landscape-scale impacts of specific industries mimic agents of selection under which particular species, communities, or ecosystems historically evolved (Fig. 2).

Reconciling industrial land use with conservation may be achievable if managers focus on similarities between natural and anthropogenic environments at the scale of communities and ecosystems. The benefits of this approach may touch ecosystem services associated with biodiversity, as well as reduced extinction risk for particular species of conservation concern. However, from our survey of the literature it appears that considerably more directed research is required to determine the potential for reconciliation ecology and habitat analogues to provide valued ecosystem services (Oberndorfer *et al.* 2007). In contrast, we found strong evidence from both case studies and syntheses that industrial analogues of natural habitats provide important conservation habitat for many rare or threatened species. Examples from flooded aggregate extraction sites include colonization by the rare water germander *Teucrum sordium* L. at a UK quarry (Beecroft, Cadbury & Mountford 2007), use of French gravel pits by threatened migrating waterfowl (Santoul, Figuerola & Green 2004), and habitat creation for at-risk amphibians and reptiles in German gravel pits (Sinsch 1988). Similarly, dry quarries provide refuge habitat for xeric specialist species, including endangered piedmont spider species in the Czech Republic (Tropek & Konvicka 2008b), rare xeromorphic ant species in Belgium (Dekoninck *et al.*, in press), and threatened Great Lakes alvar plants such as the lakeside daisy *Hymenoxys herbacea* (E.L. Greene) Cronq. (Hannes & Hannes 1984) and the dwarf lake iris *Iris lacustris* Nutt. (Richardson, Lundholm & Larson 2010). Quarry walls provide critical nesting habitat for endangered raptors such as the peregrine falcon *Falco peregrinus* Tunstall in many parts of the world (Moore *et al.* 1997), and quarry caves can serve as valuable bat hibernacula (Lina 1993).

Such case studies demonstrate the conservation potential of habitat analogues, but compelling evidence from broader studies suggests such potential is widely realized in post-industrial environments. At Czech limestone quarries 27 of 82 observed butterfly species were nationally endangered (Beneš, Kepka & Konvička 2003), while 69 of 692 observed plant and arthropod species were red-listed, many of which were grassland/forest-steppe specialists (Tropek *et al.* 2010). Similarly, 64 of 675 plant species found to colonize flooded lignite mines in Germany were classified as threatened (Kirmer *et al.* 2008), including the rare orchid *Epipactris palustris* (L.) Crantz (Esfeld *et al.* 2008). At a single gravel pit in Germany studied over 12 years, 22 of 230 vascular plant species, 22 of 78 moss species, 38 of 106 lichen species, and 216 of 527 animal species were red-listed (Schiel & Rademacher 2008). While further study may be required to determine precisely why and how anthropogenic sites provide excellent refuge for threatened species, the fact that they do so could be incorporated into broader ecosystem management policies immediately.

Synthesis: reconciling anthropogenic habitats with their natural analogues

For most distinct types of habitat or ecosystem there is a regional pool of species with potential to colonize any particular site and tolerate environmental conditions presented by the local ecosystem (Taylor, Aarssen & Loehle 1990). Urban or industrial sites can be colonized by a consistent set of species also found in natural habitats (Ursic, Kenkel & Larson 1997; Tomlinson *et al.* 2008) suggesting that conditions offered by the artificial habitat are close enough to the natural analogue to support the species, and that dispersal limitations have been overcome, allowing members of the regional pool to reach local sites. For urban and other human-disturbed ecosystems, the species pool of available colonists has long been recognized as biased toward particular natural ecosystems previously rare in most landscapes (Marks 1983; Wittig 2004; Lundholm & Marlin 2006).

In some cases the physical or chemical characteristics of natural and artificial ecosystems only partially match, as illustrated by artificial structures in marine environments. While harbour structures built from sandstone attracted biota characteristic of natural sandstone reefs, structures built using novel materials or designed to float rather than attach to the sea floor attracted novel assemblages due to species-specific substrate preferences and differences in light, exposure, and propagule availability (Connell & Glasby 1999; Holloway & Connell 2002; Bulleri & Chapman 2010). Recognizing the novelty of seawalls, Chapman & Blockley (2009; Bulleri & Chapman 2010) added a microhabitat feature, rock pools, to seawalls, and showed increased native species diversity after this ecological engineering intervention, thus shifting the habitat from a state of novelty towards conditions more analogous to natural habitat (moving from the upper right quadrant to the upper left in Fig. 1). Incomplete matching may arise from creation of structures with no regional equivalent, such as marine breakwaters in areas barren of natural hard substrates

(Bacchiocchi & Airoldi 2003). A similar phenomenon occurs in terrestrial environments on building walls: whereas stone walls are commonly colonized by species assemblages from natural rock outcrops, walls comprised of steel or glass resist colonization by the typical wall flora (Woodell 1979; Larson, Matthes & Kelly 2000).

Dispersal processes play a large role in determining which species colonize anthropogenic environments (Rishbeth 1948; McKinney 2006; Kirmer *et al.* 2008; Williams *et al.* 2009), and part of the novelty of urban ecosystems may arise from the combination of potentially-suitable native species failing to disperse from natural habitats plus high propagule pressure from non-natives that have become regionally common due to agriculture and other land-uses (La Sorte, McKinney & Pysek 2007). The main competing viewpoint to the ecosystem analogue perspective is that weedy or opportunistic species dominate novel ecosystems because they are plastic enough to handle novel conditions (Kowarik 1990; Hill, Roy & Thompson 2002). However, controlled propagule-addition experiments necessary to test this are rare, and successional patterns at some industrial sites suggests stress tolerance rather than ruderal strategies structure communities in anthropogenic ecosystems (Rehounková & Prach 2010). Evidence to date suggests that dispersal limitations can mask the potential fit between abiotic characteristics and biota from analogous habitats. Italian cities, for example, differ substantially in their urban floras, with similar urban habitats sharing species with varying local ecosystems rather than other cities in the region; however, in extreme-stress urban hardscapes, native plant species richness is high and composition represents regionally occurring rock outcrops (Celesti-Grapow & Blasi 1998).

The ecosystem analogue idea presented here suggests that another reason for the predominant role of European plant species in the homogenization of global urban floras (McKinney 2006) is that the long history of urbanization in Europe led to massive expansion of ideal habitat for species that were once restricted to naturally open environments such as rock outcrops, dunes and mudflats (Wittig 2004). Likewise, in post-industrial landscapes, proximity to appropriate natural habitats with species capable of colonizing the harsh environment determines the similarity between assembling communities and natural analogues (Novák & Konvička 2006; Kirmer *et al.* 2008; Herath *et al.* 2009). Detecting habitat analogues may thus require artificial propagule addition to assess roles for dispersal limitations on community assembly. Species available in regional pools may be able to colonize if dispersal barriers are overcome, and naturally unproductive high-stress ecosystems may provide potential analogues for multiple urban and industrial ecosystems.

Critical future steps in reconciling anthropogenic habitats with their natural analogues may require improving the match between imperfect analogue sets through intentional replication of natural habitat features in the anthropogenic environment. This is already being done in quarry rehabilitation where cliff-face walls are being drilled with holes to support climbing vegetation (Wang, Wu & Liu 2009), and in cities where buildings are fitted with eyries for birds of prey, and green walls are constructed to maximize rooting space and irrigation potential for plants, imitating the heterogeneity of natural cliff faces and increasing plant species diversity (Larson, Matthes and Kelly. 2000; Köhler 2008). Green roof substrates can be varied to increase heterogeneity and habitat diversity for plants and arthropods (Grant 2006), thereby more faithfully replicating a heterogeneous natural analogue to low productivity grasslands, tundra or rock outcrops within an otherwise homogeneous urban ecosystem, while providing a variety of other ecosystems services such as urban temperature reductions (Oberndorfer *et al.* 2007).

The research reviewed here suggests that while urban and industrial ecosystems have been heavily altered by people, individual habitat patches are not always perceived as novel by colonizing organisms. The degree of ecological novelty can thus be independent of the degree of human influence (Fig. 1). Ecological novelty can also be generated in the absence of human influence: natural long-distance colonization events, biotic interchanges produced by large-scale geological changes, and natural genetic mutations can all create novel selection pressures from the perspective of the original biota at a site. However, the hallmark of human ecology may be the production of ecological novelty at a rate that scales with our technical prowess, population growth and energy use. Nevertheless, whether as a byproduct of other activities or resulting from the purposeful construction of particular environments, humans have created artificial habitats analogous to natural ones, dictating that a novelty continuum be considered when determining management goals for anthropogenic ecosystems (Effland & Pouyat 1997).

In addition to the potential utility of this concept for supporting native biodiversity within anthropogenic ecosystems, understanding the negative side of ecosystem analogues may provide insight into major global health and economic problems related to pest and pathogen habitat expansion. Such expansion can arise through replication of key ecosystem features, from standing water in containers or soil hollows – required by pathogen-vector mosquitos (Mutuku *et al.* 2006) – to 'rock outcrop' habitat for pigeons on urban buildings (Larson, Matthes & Kelly 2000). Recognition of ecosystem analogues may help mitigate threats represented by pest species, informing management steps such as adding natural predators to water containers potentially hosting mosquito larvae (Nam *et al.* 2005), making these more similar to natural water bodies, or incorporating pigeon deterrent structures onto building ledges. Similarly, nuisance Canada geese *Branta canadensis* L. exploit urban parks and playing fields (similar to natural tundra and grassland feeding grounds), but simple interventions such as planting shrubs to alter take off angles can reduce goose use of such habitats (Conover 1991). In such cases, intervention is required to increase ecological novelty to decrease suitability for pests (moving from the upper left to the upper right quadrant, Fig. 1).

The habitat analogue concept synthesized here could function as an organizing framework for reconciliation ecology. While Rosenzweig (2003) makes a compelling argument for the need to utilize heavily managed and anthropogenic habitats for biodiversity conservation (supported by engaging case studies), here we present a potential organizing principle for research in reconciliation ecology. While Rosenzweig (2003) is not sanguine about the habitat value of the urban hardscape, the habitat analogue concept suggests that cement may actually have high biodiversity potential, though ecological engineering may be required to make artificial ecosystems more analogous to natural ones. The habitat analogue concept presents one road to reconciliation ecology in heavily modified urban and industrial landscapes: there may be more analogues than previously acknowledged, and these may be exploited to the benefit of people and native biodiversity (Oberndorfer *et al.* 2007). Specifically, there seems to be great value in greater recognition of natural rock outcrops as habitat analogues of urban and industrial hardscapes. These ecosystems represent natural refugia for biodiversity (Larson, Matthes & Kelly 2000), and a key goal of reconciliation ecology could be to transform artificial 'rock outcrops' into biodiversity refugia. This idea is especially valuable because abiotic changes wrought by urbanization are similar globally: similar habitats are being constructed everywhere (Williams *et al.* 2009). We do not suggest that the habitat analogue concept should underlie all attempts at reconciliation ecology, simply that existing patterns of biodiversity in urban and post-industrial areas suggest the utility of the concept, provided that experimental tests can be done which ascertain the roles of dispersal and habitat matching in allowing native species to colonize artificial substrates.

Conclusions

Several key principles emerge from this review of the literature. Human influence on ecosystems does not always result in functional novelty (Fig. 1) and thus should be evaluated from a 'species-eye view'. Likewise, local or regional novelty need not imply global novelty, as many non-native urban species are native to analogous habitats on other continents (Lundholm & Marlin 2006). Novelty at one scale may represent analogy at another; while hard surface environments can be analogues of natural rock outcrops, the same phenomenon occurs with many other types of artificial habitats. Finally, considerations of landscape processes such as fragmentation and dispersal need to be combined with knowledge of ecosystem characteristics within patches, and minor alterations to artificial environments can greatly facilitate colonization and habitat use by native biodiversity. The apparent novelty of some communities in urban or industrial areas reflects colonization from species pools representing potentially novel geographic areas relative to those historically drawn upon, due to severely altered abiotic conditions at anthropogenic sites. Ecosystem analogues have existed for hundreds or thousands of years in urban and industrial landscapes and should not be ignored in projections of a 'no-analogue future'. Indeed, some of these may prove resilient in the face of future global change and suggest ways of adapting anthropogenic ecosystems toward a reconciliatory ecology.

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Received 5 March 2010; accepted 15 July 2010
Handling Editor: Jos Barlow