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# INVITED ESSAY

## Green roofs may cast shadows

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A "green roof" is a roof on a structure created by humans, which has a plant community (and various hangers-on) established on it. There are many potential benefits of green roofs, ranging from moderation of local microclimates to modulations of storm runoffs, and green roofs may serve the enhancement of biodiversity conservation, as well. Green roofs would seem to be quintessential examples of a "novel ecosystem". Here, I first outline some dimensions of the novelty that warrant more research. Green roofs can provide many opportunities for creative ecological research in the assembly, dynamics and functioning of novel ecosystems. Then, I briefly discuss some potential biodiversity hazards that are created along with green roofs. Recognizing these potential "shadows" of a green roof by no means belies the strong and compelling rationale for promoting green roofs, in terms of sustainability and livability of human structures; instead the points I raise are simply issues which should be evaluated and quantified when promoting green roofs broadly as a design strategy in new buildings or retrofitted existing structures.

**Keywords:** green roofs; spillover effects; cost-benefit analysis; local adaptation; landscape perspectives

### Introduction

Strolling down Broadway, New York City recently, wading through the jostling crowds at seemingly every step, I came across for the first time the new enclosed public space at Lincoln Center, the David Rubenstein Atrium. Despite being entirely an interior volume, the Atrium has along two of its sides, lovely green walls – vertical gardens with ferns and flowering plants that bring a cascade of life to its vast open space. Beyond being a living, breathing work of art in its own right, which one could admire for its aesthetic quality (which provides sufficient justification for its existence), there were many evident benefits of this green wall. The psychological effect of sitting in the atrium was to me calming, a balm after the hubbub of the busy New York City streets just outside. The air even smelled better than it did outside, maybe because there was a bit more oxygen or less carbon dioxide in the space, or because the green biomass had filtered out toxicants (Claudio 2011).

In like manner, green roofs, though not quite as visible and so not as immediately potent as aesthetic objects as are green walls, have many potential benefits (Oberndorfer et al. 2007; Forman 2014), a number of which are discussed in impressive detail in the papers collected in this special issue of the *Israel Journal of Ecology and Evolution*. A green roof is basically a roof that has vegetation living on all or part of it. Given that urban areas comprise between 1% and 3% of all land areas on the planet, and that roofs make up about a quarter of this area (Akbari et al. 2009), and that with the burgeoning human population urban areas will only grow, green roofs are potentially a significant habitat for life. To put this in perspective, the endemic plants of serpentine soil in California are legendary, but these soils comprise only a comparably small percentage of the land area of California (Harrison & Rajakaruna 2011, p. 68). Green roofs can be a key dimension of a "green infrastructure" of urban environments (Pickett et al. 2013, p. 481), and as Rosenzweig (2016), Lundholm (2016), and others in this special issue observe, the new ecosystems created by green roofs could potentially be a useful tool for preserving biodiversity. Such benefits complement many others (Nash et al. 2016), such as aesthetic rewards for city-dwellers (apartment dwellers in mid-city could just walk upstairs to get a whiff of something natural), absorption of pollutants, modulating runoff from storms (Thuring & Dunnett 2014), changing microclimate conditions, even up to moderating temperatures by several degrees over entire cityscapes and improving the energy efficiency of buildings, and (somewhat astonishingly) indirectly facilitating solar energy capture (Nash et al. 2016; Schindler et al. 2016).

I think that on balance (and rather decidedly), the widespread implementation of green roofs would enormously enhance lives of the human residents in most urban environments, and also potentially contribute to the maintenance of biodiversity. Non-green roofs are far more devoid of life than even harsh deserts (or indeed

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almost any natural ecosystem), and some life – any life – is surely better than no life. Over half of the human species now live in urban settlements (United Nations 2015), and green roofs can potentially greatly enhance the quality of life of urban dwellers. In rural settings, green roofs could help human structures blend better into the surrounding landscape. What I will do in this essay is first present some thoughts to complement the perspectives provided in the papers by Rosenzweig, Lundholm, Kinlock et al., Thuring and Grant., and Vasl and Heim (2016) on the relationships between green roof science and basic community theory. Then, acting as a contrarian, I will reflect on some of the potential costs and risks of green roofs. By being aware of such issues – a range of "shadows" cast by green roofs – practitioners can judge their quantitative importance (which may often be negligible), and then act to avoid or at least mitigate them.

## Green roofs as novel communities and ecosystems

There are several ways one can categorize green roofs (e.g., extensive vs. intensive). One that I think may be particularly useful to keep in mind is the distinction between those green roofs (in terms of the plant assemblages) that are self-regenerating, in that populations of plants reproduce and thus recruit locally, and those that cannot reproduce *in situ*, but instead depend entirely on replanting and continual care of plants as a form of perpetual gardening on top of buildings (these of course are two ends of a spectrum). Many of my comments below assume that to at least some degree, green roofs can be constructed so that some of the taxa there (not necessarily the plants) can reproduce and generate dispersive propagules. Also, a number of my thoughts, I should acknowledge at the outset, echo the excellent compilation of papers in this special issue.

As noted by several authors, green roofs as a habitat category can be viewed as an ensemble of ecosystems that are novel, where the latter term is defined as follows:

> "A novel ecosystem is a system of abiotic, biotic and social components (and their interactions) that, by virtue of human influence, differs from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management" (Hobbs et al. 2013).

Even if humans intensively manage and control the assemblage of plant species on a green roof, other taxa, ranging from microbes to nematodes to commensal invertebrates will surely colonize (along with some plant species), outside such management, and widely-ranging species such as birds and butterflies can visit or even set up house. Both deliberately introduced and naturally colonizing species will face many novel features on a green roof (a number noted by authors in this issue), all of which can influence the capacity of roofs to sustain biodiversity. Although most green roofs involve the deliberate introduction of plants, it might often be sensible to introduce non-plant taxa, such as inocula of mychorrizae or soil fauna, as well (Rumble & Gange 2013; Molineux et al. 2014, Kadas, pers. comm.). The next few paragraphs attempt to outline some dimensions of the novelty of green roof ecosystems.

The term "novel" here is not a pejorative, but rather a descriptor. As an aside, one might wonder what "natural" means anymore, as a yardstick against which one assesses "novelty", given that most ecosystems are influenced one way or another by humans – by climate change, invasive species, nitrogen enrichment, top predator loss, and so on. But with all due apologies to George Orwell, "All ecosystems are perturbed by humankind – but some are more perturbed than others." Ecosystems where humans pick all the dominant plants and craft the "bedrock" and initial soil conditions, such as green roofs, are surely at one end of a spectrum of novelty among ecosystems.

### *Novel physical conditions*

Green roofs present novel environments to many potential deliberate or accidental colonists (Kinlock et al. 2016). In many regions, such as the temperate rainforest of the Pacific Northwest of North America, the relatively harsh conditions found on green roofs will prevent establishment of the majority of the plant species found in the typical lush natural environments in those regions (Nagase & Dunnett 2013), though there may nevertheless be some taxa available with shallow roots, or that live in special local microhabitats. It would be a valuable exercise to carefully characterize the dimensions of novelty of the physical environment of green roofs. Here are some tentative thoughts towards that end.

Green roofs might be a fair approximation of normal conditions in some microhabitats in a region, but radically different for others, even in the same region. Consider, for instance, the increasing recognition of the importance of aboveground—belowground linkages for understanding community dynamics and ecosystem processes (Kardol & Wardle 2010). The soil of course is the milieu of all belowground processes. Natural soils are highly variable among ecosystems; some are very deep, others shallow. In the Piedmont of Georgia in the southeastern US, there are distinctive plant communities found on flat granite outcrops (Shure 1999). The microenvironment is likely not so different from that expected on a roof – very hot on clear summer days, dry much of the time, windy, and with an impermeable rock substrate below a very thin layer of organic soil. Standing on an outcrop, one historically could have seen not far away stands of longleaf pine – whose taproots can penetrate up to 7 meters straight down (Longleaf Alliance 2015), although a few meters is more typical (Heyward 1933, Putz, pers. comm.) – with an understory of wiregrass and many herbaceous species, all maintained by recurrent fire. The roof's physical environment is radically different, in terms of its soil structure and absence of fire (at least one hopes!), among other features, from that of the longleaf pine ecosystem, and it seems unlikely that species adapted to the latter could thrive or even persist on a green roof. Even in some arid ecosystems, the roots of shrubs of modest aboveground stature penetrate very deeply into the earth (e.g., many plants in the Chihuahuan Desert send roots down several meters, Gibbens & Lenz 2001). "Extensive" green roofs have very shallow soil substrates ($<10$ cm), with a physical structure that would preclude roots plunging much at all (see Figure 1 in Thuring and Dunnett 2014 for a soil profile). Even "intensive" green roofs with deeper soils may not be nearly as deep or heterogeneous as in the natural soils found across much of the globe. So, one would expect any plant community sustained on green roofs to systematically differ from those on natural soils.

The soil that sustains natural communities often has emergent properties strongly influenced in its structure by, for instance, erosion of bedrock, or depositional processes actively interacting over a long period of time of pedogenesis with the resident community (Jenny 1994), including the impact of soil fauna such as earthworms. By contrast, the soil on a green roof will always be a human implant, with a distinctly different structure than natural soils. Even if one were to scrape the patches of soil off a granite outcrop and use that to start a green roof, the texture of vertical and horizontal heterogeneities in that soil will surely differ from that in the source habitat. Plant species often interact belowground, and such interactions will be constrained on green roofs. For instance, partitioning of soil water resources by plants differing sharply in root depths is less plausible as a mechanism for coexistence of different plant functional types on green roofs (though green roofs can be built with purposely variable substrate depths, see Thuring and Grant 2016). Soil fauna has many direct and indirect impacts on plant dynamics (Huhta 2007), and without deliberate introductions, green roof soils could lack key members of the soil fauna (e.g., earthworms); and, the relatively harsh physical environments of green roofs will likely further modulate the composition of soil communities by filtering potential colonists that arrive on their own from regional source pools.

So even if a green roof on the surface initially looks like the spitting-image of some local plant community, it is likely the soil community will be quite different, which ultimately would feed back to affect aboveground processes as well. As noted above, there may well be some local communities (e.g., in deserts of Israel with very shallow soil, or rock outcrops in more mesic places), where species are to a fair degree "preadapted" to green roof conditions. Even if these are utilized in planting a green roof, novel combinations of physical factors (along with other processes touched on below) could lead to novel communities. One hint of this novelty is suggested in an interesting study in New York City which compared the soil fungi on experimental green roofs (where the plants were drawn from nearby native prairie and outcrop communities), to the soil fungi on nearby ground-level city parks (McGuire et al. 2013). Almost half of the species of fungi on the roofs were not found in the parks, and the authors suggest this is due to the harsh physical conditions and shallow soil of the roofs, compared to the parks. It would be interesting to examine in like manner the soil fungal assemblages of the native prairie and rock outcrop habitats from which the green roof plant communities were drawn. The chemical and physical properties of the roof environment one might predict would lead to systematic signals in the soil communities, compared to the natural environments from which the vascular plants cloaking the roof had colonized.

Many of these points have been made in various ways by the papers in this special issue (e.g., Kinlock et al. 2016), but there are implications that I will return to below, specifically for self-regenerating green roofs. Understanding how the physical environments of green roofs will impact biodiversity within – or among – roofs requires one to gauge, quantitatively, the factors (including, in particular, environmental heterogeneity at different spatial and temporal scales) that maintain diversity in ecosystems in the first place – and the issue of species coexistence is not as yet really settled science, as exemplified, for instance, by the continuing raging debate about niche vs. neutral perspectives in community ecology.

### *Community history*

One metric of the "naturalness" of a community is the degree to which the species there have been introduced by humans. The species composition of green roofs (in contrast to "brown roofs", Kinlock et al. 2016) will not be determined by the chance vicissitudes and spatially structured pattern of colonization from near or distant source pools – as in community assembly on oceanic islands and natural habitat patches – but rather by deliberate introductions, and even likely management of population dynamics, post-introduction (e.g., weeding *Sedum* beds). This of course is not inherently dissimilar to some other arenas of applied ecology, such as restoration, but may be more extreme because of biases in which species are introduced. Thuring and Grant (2016) argue that a serious issue in green roof technology is the homogenization of species composition, say to *Sedum* and little else across many locales, due to human decisions, and sensibly argue that much more attention needs to be paid to utilizing native species, and indeed native associations of multiple species. This could facilitate conservation, at least at a local level, for some taxa. However, even here, the initial establishment of a green roof will likely be drawn from a biased subset of the regional species pool, filtered by species availability, ease of cultivation, and, in particular, the ability of the species to survive at all in the physical conditions of the green roof environment.

There is increasing evidence that the contingent history of which species arrive during community assembly can have a huge impact on community dynamics and composition, and this can contribute to biodiversity conservation via beta diversity (Fukami 2015). Green roofs might have a reduced signal of contingency, because deliberate human agency plays a much larger role in setting the initial conditions than in natural systems. Green roofs of course are one of many elements in urban environments such as greenways and highly managed city parks (Forman 2014), and these other habitats can also be dominated by non-native cultivated species (e.g., the grasses on most lawns) reflecting deliberate human agency (Gurevitch, pers. comm.). One could imagine green roofs also becoming more prevalent on structures that dot largely rural settings (as did the sod houses of the early prairie settlers in the United States), and in these settings, the novelty of the initial community assembled on the green roof will likely be even more apparent. One serious issue (Kinlock et al. 2016; J. Gurevitch, pers. comm.)

is that green roofs that utilize non-native species may provide conduits for species' invasions.

As Rosenzweig (2016) argues, the implementation of green roof technologies can be viewed as a kind of gigantic multi-part experiment, where one can potentially assess the importance of contingent assembly processes along with the utility of other aspects of current community theory. Creative experiments such as those reported in McGuire et al. (2013) provide a real opportunity to assess some basic theories in community and ecosystem ecology.

### *Constraints on community complexity and trophic interactions*

Vasl and Heim (2016) discuss how our knowledge about the maintenance of species diversity in natural communities can be applied to green roof assemblages. Broadly speaking, for species to coexist, their basic fitness in a given environment cannot differ too greatly, and negative density dependence needs to be focused more strongly within, than between, species. The latter generally requires niche differentiation between species, often in responses to environmental variation in space and time (Chesson et al. 2004). In natural plant communities, there can be substantial variation in soil properties at fine spatial scales, which provides an opportunity for niche partitioning in seedling germination requirements or rooting depth (Lechowicz & Bell 1991), and fine-scale heterogeneity is believed to underlie the incredible diversity of many soil communities (Berg 2012). Roof environments seem unlikely to have as pronounced a scale of microscale variation that can promote coexistence (though a modicum of such heterogeneity could be deliberately incorporated as a design principle). Moreover, the species composition of natural vegetation can be profoundly influenced by a range of interspecific interactions which are likely to be greatly different, or even absent, on many green roofs. In grasslands and savannas, and indeed many other biomes, plant dynamics can in large measure be driven by large-bodied grazing and browsing herbivores (Terborgh & Estes 2010). It is implausible that large herbivores will be heard pounding across green roofs anytime soon (though rumor has it that wild boar do sometimes rummage on accessible green roofs in Israel), so, in this respect, the plant communities developing there will be quite novel, and herbivore-mediated coexistence unlikely. Invertebrate herbivory might play a more dominant role on green roofs (Gurevitch, pers. comm.). Understanding the implications of this shift in herbivore regimes could be an interesting arena for future studies (Blaustein, pers. comm.). Likewise, there is a growing appreciation of belowground mutualists, and, in particular, mycorrhizae, as determinants of plant species interactions and ecosystem processes (Wall & Moore 1999). Even if an entire assemblage of a green roof were drawn from local plant species pools, and the initial relative abundances of that assemblage closely matched source communities, the initial absence of key non-plant interactors (herbivores, seed dispersers, soil mutualists and pathogens, and so on) and their subsequent filtration from the regional species pool (e.g., McGuire et al. 2013) would surely imply that the roof community would follow a quite different trajectory over time than would a comparable plant community with its full ensemble of non-plant interacting species. It would be valuable to make some *a priori* predictions about how ecosystem and community properties will unfold as a green roof develops over time.

### *Novel spatial structure and dynamics*

Local community structure arises from the interplay of local interactions, physical conditions, temporal heterogeneity, and spatial processes. An ensemble of roofs in an urban landscape will have dynamics over several timescales. For any given roof, there will be an initial introduction of plant species by humans, which might not be at all related to the relative abundances or spatial patterning of local species pools. Spontaneous assembly (Lundholm 2016) could contribute to the biodiversity conservation value of green roofs, but in an urban setting at least, roof communities are more likely to be comprised of deliberate introductions, supplemented by colonists from adjacent roofs, or parks or lawns, or ruderals from disturbed sites (Kinlock et al. 2016) than spontaneously from less disturbed and likely distant nature reserves. In towns and cities, if most buildings have green roofs, these will comprise a metacommunity of distinct "islands" of roof habitat, akin to say an oceanic archipelago, separated by a somewhat inhospitable matrix (of parking lots and the like rather than salt water). McGuire et al. (2015) have recently observed that dispersal limitation could influence the microbial assemblages that emerge on the island-like habitats of green roofs, and Aloisio et al. (2015) found that vascular plant colonization can occur, comparable to islands or habitat patches. Landscape experiments exploring habitat fragmentation have found strong effects, relative to continuous habitats, due to both disrupted connectivity and the magnification of edge effects (Haddad et al. 2015), and maybe it would be useful to think of a set of rooftops as a kind of habitat, fragmented *ab initio*, where connectivity among roofs and between roofs and other habitats should be a central concern. To play a significant role in biodiversity conservation, one ideally should view green roofs not one-by-one, but as a spatial ensemble of potentially connected habitat patches in anthropogenic landscapes, interacting with and influenced by other kinds of urban and rural environments (as in restoration ecology, Handel 2015).

And roofs have a finite lifetime. Buildings have a life cycle, and many buildings that are seemingly perfectly sound are sadly demolished because of changing economic circumstances and aesthetic tastes. O'Conner (2004) somewhat shockingly reports that the average age of non-residential buildings in Canada was about 18 years, and that the life span of office buildings in Japan was between 23 and 41 years, and notes "service lives of most buildings are probably far shorter than their theoretical maximum lives." Life cycle assessments for single-family homes often assume an average lifespan of the house of

50 years (e.g., Bribian et al. 2009). Such time spans are short, relative to that required for most plant communities to reach quasi-equilibrium, unless ensembles are largely comprised of short-lived species, and dispersal limitation is insignificant. Roof communities are likely to be in a permanent state of disequilibrium (at least in modern urban landscapes, rather than say ancient buildings), which may make application of ideas from coexistence theory dependent on equilibrial assumptions at local scales inapplicable to biodiversity maintenance. Green roofs could still contribute of course to regional maintenance of biodiversity (e.g., by providing "stepping stones" of early successional species, or feeding sites for mobile consumer species). There is a growing interest in ecology in understanding the implications of transient dynamics (Hastings 2004; Caswell 2007), and analyzing ecological dynamics on green roofs will likely mandate such non-equilibrial perspectives.

The above thoughts are meant to help provide directions for possible future research on green roofs, and some issues worthy of consideration when attempting to delineate the degree to which they are truly novel communities and ecosystems, or not, in comparison both with other urban ecosystems, and with other more natural systems.

## Costs and risks of green roofs

As noted above, I think that green roofs are basically a terrific development in architecture and urban and exurban planning. But it might be useful to think carefully about various costs and risks potentially associated with a burgeoning of green roofs. So, for the next few paragraphs, I will play "Devil's advocate" in focusing on a few possible "shadows" that green roofs might cast.

### *Economic*

"There is no such thing as a free lunch" (popularly ascribed to the free-market absolutist economist, Milton Friedman, but the author is actually unknown; Martin 2015). Building and maintaining green roofs will have obvious costs, both in terms of funds expended, and time invested. In some cases, these costs may pay for themselves (e.g., due to reduced electric bills for summer air conditioning, or the increased property value that is provided because of the esthetic or other benefits of green roofs), but in others, maybe not. If public funds are used to promote green roofs (e.g., for public buildings, such as schools, or subsidies for private structures), then these funds must be diverted from something else. One could well imagine that prudent city commissioners would trim budgets for parks and reserves in order to pay for green roof construction and maintenance on public structures. The values of green roofs on public buildings are a form of public good, which like such goods could warrant taxation. In both the public and private sector, one can predict that costs of green roofs will be minimized, which could favor utilization of a small roster of easily grown and maintained plant species, and the economies of scale that go along with homogenization (and ecological theory about community organization, ecosystem function, and biodiversity maintenance be damned, by neglect; assuming that people even care about biodiversity). If individual homeowners maintain green roofs, the cost of this maintenance (both in terms of funds, and the investment in time) has to come from somewhere else. Maddox (2015) contains a thoughtful set of commentaries about the economic costs and benefits of green roofs.

### *Ecological*

As noted above, a green roof many not be an isolated island, but instead one in an entire archipelago of roofs, interlocked by dispersal not just among themselves, but to the broader landscapes including natural and anthropogenically modified habitats. Some species of plants on green roofs can potentially produce dispersive propagules, and so enter into a regional ecological dynamic. Kinlock et al. (2016) cogently argue that green roofs can facilitate the proliferation of invasive species. Invasive species are typically defined as species that have not been historically part of a regional species pool and have become widespread and abundant. So what if we avoid this, because all plant species used on a green roof are drawn from a local native species pool? There still could be a more subtle perturbation of natural ecosystems, because some plant species will surely be more dominant on green roofs than on others, either because of biased introductions, or because some species simply do much better on roof environments. This means that dispersing propagules from those species will tend to be favored over other less abundant species in local regional metapopulation and metacommunity dynamics. Consider a single patch, where a species is persisting, in that, on average, its local births match its local deaths, so its numbers are fluctuating around some locally determined "carrying capacity". Now imagine a surge in input of seeds into that habitat, due to the proliferation of seeds being produced across an ensemble of green roofs. This enhanced input will boost population numbers above local carrying capacity. This species will then be a more effective competitor with other taxa, which do not similarly enjoy a boost in recruitment. In metapopulation dynamics, species dominance can also arise because of enhanced colonization rates (a species that first gets to a site might enjoy a priority effect in competing with other species), so again having a reliable pool of green roof populations may tilt the balance towards a subset of species in dynamic landscapes with succession, recurrent colonizations, and local extinctions. This might be particularly problematic when green roof communities are comprised of non-native species. For instance, again as a hypothetical example, *Sedum* mixtures used to establish green roofs might lead to the introduction of non-native species that can compete with native *Sedum*. Nevius's Stonecrop (*Sedum nevii*) is a rare endemic plant found on a few steep bluffs along the Chattahoochee River of Georgia, Alabama, and Tennessee. It is already threatened by an invasive, the Japanese honeysuckle. Riverbanks in hilly country are highly desirable places for housing developments, because people like to look over water (Orians 2014). If the countryside becomes replete with green roofs dominated by exotic *Sedum* – which have small, wind-dispersed seeds – there might be a heightened risk for the native, because of the abundance of this non-native competing species maintained as reservoir populations on nearby green roofs.

Such spillover effects could be mitigated by planners, for instance by building into zoning laws restrictions on green roofs near parks and reserves, providing a buffer hampering spillover, or devising regulations that make it more difficult to propagate non-native, potentially invasive species. But even here, there could be negative landscape spillover effects of green roofs onto remnant natural habitats. Consider a scenario where green roofs contain species which produce edible seeds or fruits, and where native plant communities rely upon wintering migratory birds as dispersal agents. If population sizes of wintering birds are determined by density dependence of their breeding grounds, then a fixed "pot" of birds will be distributed across available habitat patches on their wintering grounds. An increase in the green roof area could draw away birds from patches of more natural habitat, and reduce dispersal rates for those plant species found there, or the impact of these mobile birds as predators on herbivorous insects. The same point of course pertains to other urban habitats, such as urban gardens with fruit trees, which can lure migratory birds away from other sites along the migratory route and expose them to free-ranging domestic cats (a source of huge mortality for birds, Loss et al. 2013).

I have no idea if these effects are quantitatively important. One could craft alternative scenarios that point in the opposite direction. For instance, maybe the species of *Sedum* used on green roofs are drastically endangered in their native ranges, so establishing these species on roofs could help global conservation. Or, there might be no significant seed output from green roofs, so they are demographically irrelevant in terms of immigration into other habitat types. Or, provisioning of resources for resident pollinators or migratory frugivorous birds could help conserve these species in an urban environment, and these positive effects may be vastly more beneficial than any negative feedbacks. My basic point is that to understand the potential value of green roofs for biodiversity conservation, one needs to take a broad, regional perspective (where "region" is defined by the dispersal capabilities of the species involved in green roof communities), including coupling of habitats by dispersal and behavioral choice, and be careful to have an honest accounting of both potential costs as well as benefits.

### *Evolutionary*

Because of all the factors discussed above under the theme of "novelty", those species that are able to become established on green roofs are likely to face selective environments that differ in major ways from their ancestral environments. For components of green roof ecosystems that are self-regenerating (i.e., that reproduce), there is thus the potential for adaptation by natural selection to the novel conditions on green roofs. Reproduction that is not strictly vegetative creates propagules that can disperse beyond the natal habitat. So, in addition to novel evolutionary trajectories within any given green roof, there can be gene flow among them, and beyond them to more natural habitats outside. This is not in itself inherently bad, and may basically just boost overall genetic regional diversity, but it is useful I think to contemplate potential negative side-effects that might occur in some circumstances.

Some years ago, I was a faculty member at the University of Kansas, where I was fortunate to have an office on the seventh floor of Dyche Hall, a lovely nineteenth century limestone building housing the Museum of Natural History. From my window, beyond the stone gargoyle on the ledge, I could see at least 20 miles across a breathtaking vista – the fields, woods, and plains of eastern Kansas. One day in the mid-1980s, I idly glanced out my window to soak in the view and was startled instead of this vista to see, a few inches from my desk, the face of my friend and colleague, the late (1925–2014) Professor Richard Johnston. His office was adjacent to mine, and there he was crawling on all fours – very carefully and methodically – along that ledge, far above the campus below. He looked up gingerly and smiled. Later, he told me that what he was doing was checking nest boxes he had put out for the feral Rock Dove (*Columba livia*) population that resided on our campus building. Most people view feral pigeons as pests – Richard viewed them as an intellectual opportunity. His ledge-crawling was just one piece of a comprehensive study of the biology of this ubiquitous commensal of our species (Johnston & Janiga 1995). Richard had a life-long interest in the biology of synanthropic organisms – those taxa which live closely associated with humankind (Johnston 2001). With Robert Selander, in the 1960s, he had carried out classic studies (e.g., Johnston & Selander 1973) of the rapid development of geographic variation in House Sparrows (*Passer domesticus)*, introduced to North America from Europe in New York City (Brooklyn) in 1852, after which they spread across essentially the entire continent. Although the species is not entirely commensal with humans (in central Asia there are populations that are found well away from human habitation), over most of its range, it is hardly ever found far from people (Dunn 2012). Richard then turned his attention to the Rock Dove, another species which is largely (if not entirely) associated with humans (Johnston & Janiga 1995). So that was what I caught him doing – documenting different aspects of the reproductive biology of feral domestic pigeons.

One idea that I recall mulling over with Richard was whether or not the evolution of synanthropy, from wild ancestors, could lead to an evolutionary feedback, where the ancestral habitat use became degraded in a given species, so that it might even abandon use of that habitat and become more or less completely dependent on its association with humans. House Sparrows, Rock Doves, among other species (e.g., the House Mouse), surely became much more abundant after they started utilizing anthropogenic habitats, and potentially their ability to utilize their original habitats faded away. An old idea in evolutionary biology is that when a species is distributed over two habitats, but is much more common in one than the other, there can be a kind of evolutionary dominance, where the species gravitates in its adaptive evolution towards the habitat in which it is more abundant. The idea is implicit in Ernst Mayr's hypothesis that gene flow from abundant central populations to sparse marginal populations could inhibit adaptation in the latter sufficiently to create stable range margins (Mayr 1963). In extreme cases, there can even be a kind of collapse in habitat use, driven by migrant load (Lenormand 2002). This scenario does not always hold (e.g., gene flow can provide the very variation needed for adaptive evolution in a marginal habitat, see Gomulkiewicz et al. 1999 for an explicit model showing this effect), but it does crop up in a range of evolutionary models.

In the context of green roofs, what this means is that if a species drawn from the local flora is utilized widely across an urban landscape, is abundant on green roofs, and reproduces there and self-replenishes, then one should plausibly expect adaptation by natural selection to the novel roof environments. This is not in itself bad and indeed might be quite welcome. Indeed, in a changing environment, genetic variation that is maintained because of adaptation to marginal or unusual conditions (such as the conditions on green roofs) might in the long run be particularly important for the persistence of species. But if some of the reproductive output of roofs is exported to external environments, then there might be a migrational genetic load imposed on natural populations in remnant habitats. So, if one's conservation goal is maintaining species, with their ancestral traits, in the original habitats of the landscape in which we found them, realizing this goal could be perturbed a bit by a proliferation of that species or close relatives on green roofs, so that across a broader landscape, adaptive evolution is altered in whatever taxa occupy the roofs – including in those habitats where one is trying to conserve nature in some kind of vague semblance to its original state. Consider, for instance, as a hypothetical example again *Sedum nevii* along the Chattahoochee River. Species in this genus are well known to hybridize across species boundaries (DeChaine & Martin 2005), and being insect-pollinated, spatially separated populations can hybridize and exchange genes over large distances. If a colony of honeybees sets up house on a Chattahoochee bluff, it could well import into the native *Sedum* genes emanating from green roofs on buildings scattered across a wide riverine landscape. This could impose a migrational load on the endemic, further endangering it. And if not, the traits of these populations may come to resemble to a degree those on the green roofs themselves – what we might call "spillover synanthropy".

Again, I reiterate that I think that the many benefits of green roofs, beyond their potential biodiversity benefits, provide ample justification for championing their use in human spaces (particularly in highly urbanized environments). But a consideration of how green roofs fit into a broader goal of biodiversity conservation should be part of an environmentally wise polity in our increasing urbanized world, and part of wisdom is objectively assessing the potential ecological and evolutionary costs and risks – the shadows, as well as benefits – of creative innovations such as green roofs.


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## References


Akbari H, Menon S, Rosenfeld A. 2009. Global cooling: increasing world-wide urban albedos to offset $CO_2$. Clim Change. 94:275–286.

Aloisio JM, Palmer MI, Tuininga AR, Lewis JD. 2015. Plant community dynamics of native plant assemblages on geographically isolated green roofs. Abstract. Available from: http://eco.confex.com/eco/2015/webprogram/Paper51816.html.

Berg MP. 2012. Patterns of biodiversity at fine and small spatial scales. In: Wall D, editor. Soil ecology and ecosystem services. Oxford: Oxford University Press.

Bribian IZ, Uson AA, Scarpellini S. 2009. Life cycle assessment in buildings: state-of-the-art and simplified LCA methodology as a complement for building certification. Build Environ. 44:2510–2520.

Caswell H. 2007. Sensitivity analysis of transient population dynamics. Ecol Lett. 10:1–15.

Chesson P, Geaurer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia. 141:236–235.

Claudio, L. 2011. Planting healthier indoor air. Environ Health Perspect. 119:A426–A427.

DeChaine EG, Martin AP. 2005. Marked genetic divergence among sky island populations of *Sedum lanceolatum* (Carrulaceae) in the Rocky Mountains. Am J Botany. 92:477–486.

Dunn R. 2012. The story of the most common bird in the world. Available from: http://www.smithsonianmag.com/science-nature/the-story-of-the-most-common-bird-in-the-world-113046500/?no-ist.

Forman RTT. 2014. Urban ecology: science of cities. Cambridge: Cambridge University Press.

Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. Ecol Evol Syst.

Gibbens RP, Lenz JM. 2001. Root systems of some Chihuahuan Desert Plants. J Arid Environ. 49:221–263.

Gomulkiewicz R, Holt RD, Barfield M. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. Theoret Popul Biol. 55:283–296.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, et al. 2015. Habitat fragmentation and its lasting impacts on Earth's ecosystems. Sci Adv. 1(2):e1500052. doi:10.1126/sciadv.1500052

Handel SN. 2015. Jump-starting the habitat engine. Ecol Restora. 33:1−2.

Harrison S., Rajakaruna N. editors. 2011. Serpentine: the evolution and ecology of a model system. Berkeley (CA): University of California Press.

Hastings A. 2004. Transients: the key to long-term ecological understanding. Trends Ecol Evol. 19:39−45.

Heyward F. 1933. The root system of longleaf pine on the deep sands of western Florida. Ecology. 14:136−148.

Hobbs RJ, Higgs ES, Hall CM. 2013. Novel ecosystems: intervening in the new ecological world order. Chichester: Wiley-Blackwell.

Huhta V. 2007. The role of soil fauna in ecosystems: a historical review. Pedobiologia. 50:489−495.

Jenny H. 1994. Factors of soil formation: a system of quantitative pedology. New York (NY): Dover Publications.

Johnston RF. 2001. Syananthropic birds of North America. In: Marzluff JM, Bowman R, Donnelly R, editors. Avian ecology and conservation in an urbanizing world. Boston (MA): Kluwer Academic Publishers.

Johnston RF, Janiga M. 1995. Feral pigeons. Oxford: Oxford University Press.

Johnston RF, Selander RK. 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. Am Naturalist. 107:373−390.

Kardol P, Wardle DA. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. Trends Ecol Evol. 25:670−679.

Kinlock NL, Schindler BY, Gurevitch J. 2016. Biological invasions in the context of green roofs. Israel J Ecol Evol. 62(1−2):32−43.

Lechowicz MJ, Bell G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. J Ecol. 79:687−696.

Lenormand T. 2002. Gene flow and the limits to natural selection. Trends Ecol Evol. 17:183−189.

Longleaf Alliance. 2015. Longleaf roots. Available from: http://www.longleafalliance.org/longleaf-pine/physiology/longleaf-pine-roots

Loss SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Commun. 4:1396. doi:10.1038/ncomms2380

Lundholm J. 2016. Spontaneous dynamics and wild design in green roofs. Israel J Ecol Evol. 62(1−2):23−31.

Maddox D, editor. 2015. Why don't all public buildings have green roofs? Available from: http://www.thenatureofcities.com/2015/08/12/why-dont-all-public-buildings-have-green-roofs-or-all-large-private-buildings-e-g-businesses-would-this-be-a-good-idea-what-would-it-take-to-make-it-happen-and-to-make-it-worthwhile/

Martin G. 2015. Available from: http://www.phrases.org.uk/meanings/tanstaafl.html

Mayr E. 1963. Animal species and evolution. Cambridge (MA): Harvard University Press.

McGuire KL, Payne SG, Oraz G, Palmer MI. 2015. Bacteria and fungi in green roof ecosystems. In: Sutton R, editor. Green roof ecosystems, Ecologicla Studies 223. Switzerland: Springer International Publishing.

McGuire KL, Payne SG, Palmer M, Gillikin CM, Kaefe D, Kim SJ, Gadallovich SM, Discenza J, Rangemannar R, Koshner JA, et al. 2013. Digging the New York city skyline: soil fungal communities in green roofs and city parks. PLOS One. 8(3):e58020/1−13.

Molineux CJ, Connop SP, Gange AC. 2014. Manipulating soil microbial communities in extensive green roof substrates. Sci Total Environ. 493:632−638.

Nagase A, Dunnett N. 2013. Establishment of an annual meadow on extensive green roofs in the UK. Landscape Urban Plan. 112:50−62.

Nash C, Clough J, Gedge D, Newport D, Ciupala MA, Connop S. 2016. Insights on the biodiversity potential of biosolar roofs: a London Olympic Park green roof case study. Israel J Ecol Evol. 62(1−2):74−87.

Oberndorfer E, Lundholm, J, Bass B, Coffman RR, Doshi H, Dunnett N, Gaffin S, Kohler M, Liu KKY, Rowe B. 2007. Green roofs as urban ecosystems: ecological structures, functions, and services. Bioscience. 57:823−833.

O'Conner J. 2004. Durability service life. Available from: http://cwc.ca/wp-content/uploads/2013/12/DurabilityService_Life_E.pdf

Orians GH. 2014. Snakes, sunrises, and Shakespeare: how evolution shapes our loves and fears. Chicago (IL): University of Chicago Press.

Pickett STA, McGrath B, Cadenasso ML. 2013. The ecology of the metacity: shaping the dynamic, patchy, networked, and adaptive cities of the future. In: Pickett STA, Cadenasso ML, McGrath B, editors. Resilience in ecology and urban design. Berlin: Springer.

Rosenzweig ML. 2016. Green roofs: new ecosystems to defend species diversity. Israel J Ecol Evol. 62(1−2):7−14.

Rumble H, Gange AC. 2013. Soil microarthropod community dynamics in extensive green roofs. Ecol Eng. 57:197−204.

Schindler BY, Blank L, Levy S, Kadas G, Pearlmutter D, Blaustein L. 2016. Integration of photovoltaic panels and green roofs: review and predictions of effects on electricity production and plant communities. Israel J Ecol Evol. 62(1−2):68−73.

Shure DJ. 1999. Granite outcrops of the southeastern United States. In: Anderson RC, Fralish JS, Baksin JM, editors. Savannas, barrens, and rock outcrop communities of North America. Cambridge: Cambridge University Press.

Terborgh J, Estes JA, editors. 2010. Trophic cascades: predators, prey and the changing dynamics of nature. Washington (DC): Island Press.

Thuring C, Grant G. 2016. The biodiversity of temperate extensive green roofs − a review of research and practice. Israel J Ecol Evol. 62(1−2):44−57.

Thuring CE, Dunnett N. 2014. Vegetation composition of old extensive green roofs (from 1980s Germany). Ecol Proc. 3:4. Available from: http://www.ecologicalprocesses.com/content/3/1/4.

United Nations. 2015. Department of Economic and Social Affairs, Population Division. World Urbanization Prospects. The 2014 Revision (ST/ESA/SER.A/366).

Vasl A, Heim A. 2016. Preserving plant diversity on extensive green roofs - theory to practice. Israel J Ecol Evol. 62(1−2):103−111.

Wall DH, Moore JC. 1999. Interactions underground: soil biodiversity, mutualism, and ecosystem processes. Bio Sci. 49:109−117.