

# Nitrogen Pollution and the Meltdown of Urban Ecosystems

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**Abstract:** Urban ecosystems are carrying an extinction debt. Mitigating this debt will require the development of a predictive framework that improves our understanding of the factors causing decline of native biodiversity in urban areas. I argue that nitrogen is a common currency around which such a predictive framework could be built. I first summarise the evidence that shows the probable extent of nitrogen enrichment in urban ecosystems. I then review the body of empirical evidence that describes how nitrogen enrichment affects ecosystem process and function. By unifying these two bodies of empirical evidence, I generate a series of testable hypotheses that may allow for a better understanding of native biodiversity loss in urban areas.

**Keywords:** biodiversity; competition; extinction; eutrophication; herbivory; nitrogen; urban ecology

## 1. Urbanisation

Humans have a tendency to build cities in locations that are naturally bio-diverse [1,2]. Urbanisation is therefore a leading cause of native biodiversity loss [3,4]. The loss of native biodiversity in urban areas is especially problematic because most of us live in cities and native biodiversity in urban green spaces is critically important to our quality of life, as it provides the ability to reconnect with nature nearby [5,6]. In response to this problem, urban ecologists have repeatedly concluded that urban ecosystems are so novel and complex that an entirely new theoretical framework is needed [2,7–10]. The fact that humans modify urban ecosystems in so many different ways (i.e., atmospheric pollution, engineered drainage, proliferation of impermeable surfaces, the urban heat island effect, deliberate importation and cultivation of exotic species) is the central argument used to support this perceived need for novel theory [7]. Here, I question the need for novel theory and suggest that urban ecosystems can be understood through the lens of existing theory. As an example, I describe how existing knowledge/theory on nitrogen enrichment and nitrogen affects a broad range of ecosystem processes can help us to understand the mechanistic basis of native biodiversity decline in urban ecosystems.

## 2. Urban Ecosystems Are Nitrogen Enriched

Reactive (biologically useful) species of nitrogen ( $N_r$ ) such as ammonium and nitrate, are critically important, but extremely rare in nature [11]. Reactive forms of nitrogen (ammonium and nitrate) are rare in nature because they are inherently unstable and prone to regress to the atmosphere into the relatively stable  $N_2$  configuration. The volatility and instability of  $N_r$  creates serious measurement challenges. The low concentrations at which  $N_r$  exists in the natural environment is a measurement challenge in itself. Further, soil nitrogen can exist in a variety of forms (i.e., ammonium, nitrate, and organic nitrogen) and different plant species may preferentially use these different forms of nitrogen [12–14]. Therefore, measuring  $N_r$  availability requires prior knowledge of which form of

nitrogen plants are using. Even armed with prior knowledge we can run into problems because whole plant communities can switch nitrogen source when soil water availability changes [15]. Rates of nitrogen cycling and therefore nitrogen availability may also vary in response to temperature, i.e., the urban heat island effect [16]. Because of these environmental sensitivities the availability of nitrogen is highly variable through space and time [17]. Nitrogen availability is also hard to pin down because it is a relative concept that depends on demand and supply [18]. Different species of plant may possess different nitrogen requirements or sensitivities [19,20]. In ecosystems historically dominated by slow growing stress tolerant trees, even a relatively modest increase in  $N_r$  may have negative impacts on ecosystem functioning [14,21]. Therefore, the question of how much nitrogen is too much for any given ecosystem is difficult to define before the fact [22]. Nevertheless, the measurement issue is not insoluble (see for example the approaches used by [23,24]) and the fact that  $N_r$  is difficult to measure does not negate the fact that urban ecosystems are subject to high levels of nitrogen pollution [19,25–28].

One of the by-products of fossil fuel combustion is reactive species of nitrogen ( $N_r$ ). Our knowledge about rates of  $N_r$  deposition in and near cities is less than adequate [29,30]. Nevertheless,  $N_r$  deposition rates are likely high in cities the world over because of the prevalence of cars, trucks and industry in cities [31]; because of the “urban scrubber” effect described by Lovett et al. [29]; and because “tall, aerodynamically rough surfaces” (i.e., buildings) efficiently trap aerosol pollutants [22]. The fact that cities are often built on ex-agricultural land is another reason for  $N_r$  enrichment. Fertilisers are commonly used to enhance agricultural productivity and this fertilisation may leave a legacy of enriched soil fertility. Legacies of enriched soil fertility are especially common for cities built on arid ecosystems [32]. Engineered drainage is another source of  $N_r$  in cities. Water logging of soils inhibits most forms of microbial metabolism. As a result organic carbon (and the associated nitrogen) deposited in soils and sediments may accumulate and persist over geologic time scales [33]. Engineered drainage in cities is reversing this process on an unprecedented scale, lowering water tables and probably changing soils from sinks to sources of  $N_r$  [34]. Fertilizer run-off from gardens and golf courses, pet waste, and leakage from sewers and septic tanks also contribute significantly to the nitrogen budget of urban areas [27]. The urban heat island is another factor that may be increasing  $N_r$  availability in urban ecosystems [16]. Higher temperatures facilitate the breakdown of recalcitrant soil carbon [35] making the nutrients sequestered in recalcitrant soil carbon available for biological processes. Finally invasive species are abundant in urban areas and these may produce dense thatches of labile leaf litter that may accelerate the cycling and retention of nitrogen [19,36]. To summarize: It is clear, for a variety of reasons, that urban ecosystems are generally nitrogen enriched.

### 3. Potential Effects of Nitrogen Enrichment on Ecological Processes

Due to the biological importance of  $N_r$  [11] the urban enrichments described in the preceding paragraph are likely having profound negative impacts on native biodiversity in urban ecosystems. For example, when the availability of nitrogen increases plants generally decrease relative allocation of biomass below ground [37]. In geographic locations where climatic water balance is variable, a relatively low root mass fraction (which can be induced by  $N_r$  enrichment) may increase the susceptibility of perennials to drought [38]. High  $N_r$  availability may also reduce the prevalence of mycorrhizal infection which may further increase the susceptibility of perennials to drought [22]. Many invasive species, in comparison, are ephemeral [39] and may avoid negative drought effects simply because of their life history schedule (phenology). Even if we consider only perennials (because some exotic species are perennial), the situation is qualitatively similar; exotic species are likely to possess relatively ephemeral functional traits [40] which means that exotic species should be better able to cope with fluctuations in resource levels [41]. Thus, natural climatic variability combined with nitrogen enrichment should favour the growth and persistence of exotic species over more perennial native vegetation.

Nitrogen enrichment also has the potential to directly impact competitive interactions between native and exotic plants. Increased resource availability increases the potential and probability of

biological invasion [42]. Competitive pressure from exotics is the most important underlying cause of native biodiversity loss following biological invasion [43], and there is compelling evidence that nitrogen enrichment intensifies biological invasions [21,22,31,44]. Nitrogen enrichment might also impact interaction networks (interactions among three or more species). Nitrate for example is water soluble and the uptake of nitrate is closely linked to transpiration [45]. Therefore when nitrogen is abundant plants can meet their nitrogen requirements with a higher degree of water use efficiency (i.e., by using less water per unit of growth). Therefore when nitrogen is abundant, and plants are meeting their nitrogen requirements with less usage of water, the soil may retain water for longer periods of time. This in turn may promote the growth of pathogenic fungi [46]. In urban environments (with many exotics), I hypothesise that the additional pathogen pressure will disproportionately affect the native flora because of the enemy release hypothesis, which predicts that invasive species have become invasive because they have left their natural enemies behind [47,48].

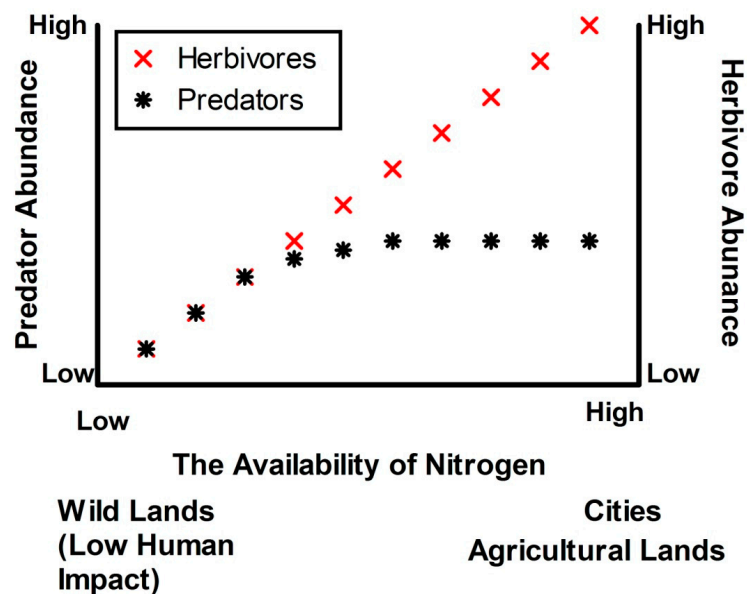
I also expect that the effects of  $N_r$  enrichment will reverberate strongly through the urban food chain. In nitrogen enriched urban ecosystems there could be a truncated flow of nutrients through the food web (more herbivores, less pronounced changes in predator abundance) (Figure 1 [49,50]). Increased availability of  $N_r$  in soil may result in high tissue nitrogen concentrations in plants [22,49,51]. Nitrogen is *the* nutrient that limits insect herbivore growth most [11]. Therefore we can expect that insect herbivores will produce more offspring and also grow larger following  $N_r$  enrichment [22,52]. Growing larger may place herbivores in size classes where they are less susceptible to attacks from predators [50,53]. A second factor that may cause decoupling of predator and herbivore production is the invasion and growth of exotic species following  $N_r$  enrichment [19,22,44]. Exotic species are abundant in urban areas and are an ideal habitat for invertebrate herbivores because exotic plants often provide invertebrates with protection from the desiccating effects of the sun, and also because invertebrates are better able to hide, and suffer lower levels of predation in microhabitats dominated by exotic species. Consistent with this prediction, previous studies have shown that the habitat provisioning effect of exotic species can be catastrophic for the survival and growth of native plants [54,55]. There is not a wealth of data on invertebrates in urban ecosystems but the available evidence is broadly consistent with the hypothesis outlined. Invertebrate herbivores are relatively abundant in urban areas [52,56–58] whereas corresponding increases in predator abundance appear to be more modest [59]. Whether decoupling of predator and invertebrate herbivore production in urban ecosystems is related to  $N_r$  enrichment is an open question [50] that requires further empirical testing. However it is a reasonable hypothesis because agricultural and urban landscapes are similar with regard to nitrogen status [27], and decoupling can explain why trophic structure in urban and agricultural landscapes (relative to wildlands) appears similar (see [49,60]).

#### 4. Predictions

The hypothesis that  $N_r$  enrichment in urban ecosystems is fundamentally altering the expression of physiological traits and trophic interactions to the detriment of native species leads to the following testable predictions:

- (1) Nitrogen (N) fertilisation will cause shifts in patterns of biomass allocation in native perennials. This will increase the vulnerability of perennial native flora to environmental variability (i.e., drought). N fertilisation will also affect biomass allocation in exotic and/or ephemeral species, but the fitness consequences will be less extreme. With regard to the ephemeral species, it should not matter if the ephemerals are native or exotic [61]. The life history schedule should be all that matters.
- (2) N fertilisation will increase exotic species growth and exotic species will have direct negative impacts on the native flora. This competitive effect should be most important in preventing seedling establishment.

- (3) N fertilisation will increase the water use efficiency of vegetation, and thereby increase soil water availability. This in turn will promote growth of soil pathogens that will exert a more negative effect on native flora in relative terms.
- (4) N fertilisation in urban ecosystems will decouple herbivore and predator production (see Figure 1) and this will limit recruitment of native species. These changes will be due to: (a) relatively dense swards of grasses affording herbivorous invertebrates protection from predators; and (b) changes in herbivore body size following fertilisation, placing herbivores beyond the size handling class of many predators. High herbivore loads will in turn limit recruitment of the indigenous flora more than the exotic flora.



**Figure 1.** At low levels of N availability the positive effects of N fertilisation flow with efficiency through the trophic web. However, as  $N_r$  pollution increases, there is a decoupling of herbivore and predator production. This decoupling is the result of: (1) nitrogen promoting weed growth, which gives herbivores a place to hide from predators; and (2) nitrogen improving the growth of individual herbivores placing them beyond the handling size of many predators.

## 5. Solutions

If, as suggested,  $N_r$  enrichment is negatively affecting native biodiversity in urban ecosystems then the management options are many and centre on extracting resources from the affected ecosystems. We may need to combine conservation with agriculture. The Bay Checkerspot Butterfly is a good example of what may be required. This species is now restricted to serpentine grasslands in California and is threatened by the combined impacts of nitrogen deposition and competitive effects of an exotic grass on the butterflies' host plant. The butterflies' continued existence is dependent on a moderate level of cattle grazing [31]. Prescribed burning may be another option. Fire, metaphorically, is a voracious consumer of nutrients [62] and long return intervals between fire have even been implicated in the local extinction of native grassland flora across an urban–rural gradient in Victoria, Australia [63]. The commonly used technique in ecological restoration of removing topsoil is another possibility [64]. In instances where resource extraction and/or prescribed burning are likely to increase invasion pressure (see [65]), soil amendment with black carbon could be another potential solution. Black carbon (biochar) can be produced to have a very high adsorptive capacity [66]. By conditioning soil in urban ecosystems with this type of black carbon we could reduce the availability of nitrogen and at the same time sequester carbon in a recalcitrant form. We could also prevent excess nitrogen from entering urban ecosystems in the first place through more rationale use of resources. Opportunities to

intervene in the nitrogen cycle are numerous [67]: we could for example use cleaner fuels or devise more efficient ways to apply fertiliser.

## 6. Conclusions

I am not suggesting that nitrogen enrichment is the sole cause of native biodiversity decline in urban areas. We know for example that fragmentation may be especially important for non-sessile organisms [68]. Native biodiversity loss in urban areas, like all real world problems is probably multilayered and complex and will require models and management prescriptions that effectively contemplate and deal with the complexity [69]. Nevertheless, the task would be resolved more easily if urban ecologists applied the hard won knowledge attained in other ecology sub disciplines. Much native biodiversity decline in urban ecosystems may be the result of nitrogen pollution. If this hypothesis is correct, then there are many already developed and effective strategies that could facilitate efforts to conserve native biodiversity in the urban matrix.

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