INSIGHTS

PERSPECTIVES

ECOLOGY

The natural capital of city trees

City trees can help to reduce pollution and improve human health

By **Katherine J. Willis**[1,2] *and* **Gillian Petrokofsky**[2]

The term "natural capital" refers to elements of nature that, directly or indirectly, produce value for people. Determining the location and quality of natural capital assets, and the ecosystem services that they provide for human well-being, is now underway in many countries, not just in the countryside but also across cities. One example of such natural capital is provided by city trees, which can take up substantial amounts of carbon dioxide (*1*) and also cause local cooling, thereby ameliorating the urban heat island effect (*2*). City vegetation can also reduce pollution and improve human health. However, understanding the characteristics of particular species is critical, and planting the wrong species in the wrong places can cause unintended problems.

Some tree species are more pollution-resistant than others. For example, the London plane (*Platanus x hispanica*) has thrived alongside city streets for many

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Trees line Park Avenue in New York City. Planting trees in cities has clear benefits for human health and pollution control.

years, partly because it has an inbuilt pollutant-cleansing process through its ability to shed its bark. Vegetation can also act as a natural filter, removing particulate matter (PM) from the air either through the interception of airborne particles or the uptake of gaseous air pollution via stomata on the leaf surface (*3*). The amount of PM removed, however, largely depends on the species. For example, Chen *et al.* recently showed that the effectiveness of different plant species in removing PM from Beijing's air (and thus their potential for helping to reduce the severe smog that plagues the city every winter) varied by up to 14 times between species (*4*).

The main reasons for this variation were differences in leaf surface area, quantity of foliage cover, and physical shape of the species. Trees were most effective at removing PM, although tree height was important (shorter trees performed better). Good PM-removing trees included species of elm, magnolia, ash, and holly. Certain species of climbing vines performed better than some trees for PM capture, an important consideration when creating green walls and green roofing on city structures. Those not so effective at PM capture included some common street species, such as ginkgo (*Ginkgo biloba*) and honeysuckle (*Lonicera maackii*) (*4*).

Deciduousness of the trees is also important, as are the size, shape, and waxiness of the leaves. Sæbø *et al.* have reported that among 27 species of trees and shrubs commonly planted in Norwegian and Polish cities (*5*), coniferous species—in particular the Scots pine (*Pinus sylvestris*)—are the most efficient at capturing PM. By contrast, broad-leaved deciduous species such as lime (*Tilia cordata,* the iconic "linden" tree of Berlin) were less efficient. An online tool developed to capture these data to assist with urban tree planting, i-Tree, developed by the U.S. Forest Service, is revealing some remarkable amounts of PM capture by different city trees. For example, a recent study using i-Tree estimated that the trees in public spaces in Strasbourg, France, removed 88.23 metric tons of pollutants between July 2012 and June 2013 (*6*).

In addition to pollution control, there is limited, but persuasive, evidence for positive effects of city trees on physical and mental health, which complements psychological research that has substantiated the benefits of parks and green spaces as health resources for urban populations (*7*). For example, when Kardan *et al.* compared neighborhoods with different densities of street trees in Toronto, Canada, with high-quality data sets on public health and demographics, they found that higher tree density (maple, locust, spruce, ash, linden, oak, cherry, and birch) was correlated with higher perception of health and lower incidence of heart and metabolic disease (*8*). The authors estimate that planting just 10 or more trees per city block is equivalent to saving more than $10,000 Canadian dollars per household in health-related costs—a figure that far exceeds the estimated cost of planting and maintaining those additional 10 trees.

Similarly, Beyer *et al.* looked at a spectrum of urban to rural environments in Wisconsin, USA, and found, after controlling for a wide range of confounding factors, that having more trees in a neighborhood (measured as a higher percentage of tree canopy) was associated with more positive mental health, particularly among those aged 55 and older (*9*). Likewise, Taylor *et al.* found that in a cross-sectional study in London, UK, areas with higher rates of antidepressant prescription and prevalence of smoking had lower street tree densities. Smoking levels were linked to levels of antidepressant prescriptions, but after controlling for confounding factors, the relationship between number of trees and prescriptions to treat depression held (*10*).

A study analyzing the effects of the loss of city trees also provides compelling evidence for the benefits of trees for human health (*11*). Donovan *et al.* compared health data before and after the loss of 100 million ash (*Fraxinus* spp.) trees across 1296 U.S. counties between 1990 and 2007 due to infestation by the emerald ash borer (*Agrilus planipennis*). They found statistically significant increases in mortality related to cardiovascular and lower–respiratory tract illnesses. The magnitude of this effect increased as the infestation progressed. The authors concluded that tree loss was associated with increased mortality related to cardiovascular and lower-respiratory systems.

However, there is a downside. Some tree species can be associated with a number of problems, notably the release of airborne pollen that causes human allergic reactions and the emission of biogenic volatile organic compounds (BVOCs) associated with ozone formation.

Trees belonging to the orders Fagales, Lamiales, Proteales, and Pinales are the most potent allergen sources (*12*). Many common urban trees belong to these orders, notably birch (*Betula* spp.), ash (*Fraxinus* spp.), mesquite (*Prosopis juliflora*), plane (*Platanus* spp.), and cypress (*Cupressus* spp.), raising the question of trade-offs between benefits and problems associated with some mass tree-planting initiatives in major cities including New York, London, and Shanghai. Trees in these campaigns are mostly chosen to reflect what is considered local, and although some advice is provided about issues such as poisonous fruit, there are almost no warnings about pollen allergy potential and other less visible health hazards (*13*). These initiatives also often neglect to take into account the production of BVOCs by street trees. Black gum (*Nyssa sylvatica*), poplar (*Populus* spp.), oak (*Quercus* spp.), false acacia (*Robinia pseudoacacia*), plane (*Platanus* spp.), and sycamore (*Acer* spp.) trees are all high BVOC emitters that are widely planted as street trees. There is a very real danger that BVOC releases could reverse the gains made in controlling anthropogenic emissions (*14*).

Finally, there is a problem with the shape of trees and their height. A number of studies have demonstrated that tall trees and dense vegetation can limit the circulation of air and trap PM at street level (*4*). In some cases, this aerodynamic effect might be more detrimental than the PM removal capacity of the trees. *Platanus x hispanica*, for example, needs to be heavily pruned, because its dense structure otherwise results in poor air flow and causes PM to become trapped at street level (*15*).

Planting trees in cities can therefore have clear benefits, but also downsides. Understanding these trade-offs requires detailed knowledge of the species concerned and their suitability to the city. Ecological tolerances of trees must also be taken into account; tropical trees, for example, are unlikely to do well in boreal zones, and this will influence their functionality in cities outside their natural range. However, the list of tree species planted in cities is fairly limited, and beauty often takes precedence over science, with little regard paid to the full range of natural capital advantages and disadvantages of individual species (*16*). When searching for new potential candidates, diversity is important; although we often cannot guard against the next pathogen, ensuring that a wide range of different trees are planted will provide some resilience. It might be good to also consider rare, threatened, and endangered species. *Ginkgo biloba* was once one of the rarest and most critically endangered species in the world; its populations are now widespread globally, thanks to its use as a city tree. ■

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NEURODEVELOPMENT

A crossroad of neuronal diversity to build circuitry

Clustered protocadherin genes control convergence and divergence of neurons

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One of the most important questions in brain science is how infinite information is processed and maintained by a finite number of neurons. A nearly limitless number of combinations and groups of neurons can be produced and connected with each other from a limited number of neurons. It is thought that a diversity of cell-surface proteins could form the basis of a molecular code for individual neuron identity (*1*). Considering the relatively small number of genes in the human genome (~2 × 10⁴), the explosive combination of different isoforms derived from each gene could contribute to such neuron diversification. In contrast to the diverse specific connections between neurons, brains also have diffuse neuronal projections that broadly regulate brain function. In this case, appropriate spacing of neurites (axon or dendrite projections of a neuron) is thought to be controlled by self-avoidance (repulsion between neurites belonging to an individual cell) and tiling (repulsion between neurites from different neurons of the same cell type) (*2*). On pages 406 and 411 of this issue, Chen *et al.* (*3*) and Mountoufaris *et al.* (*4*), respectively, provide mechanistic insights on specific and diffuse neuronal projections by focusing on clustered protocadherin (Pcdh) proteins, a group of cell adhesion molecules, using olfactory and serotonergic neural systems as models.

> ***"...the functional diversification of a gene family can be accomplished by transcriptional regulation."***

Pcdh genes are encoded by three gene clusters located in tandem on the same chromosome—*Pcdh*α and -γ have genomic structures that are similar to those of the T cell receptor's gene segments and of the immunoglobulin gene segments, in which the 3′ constant regions are spliced to variable exons (*5*). In mice, *Pcdh*α, -β, and -γ clusters have 14, 22, and 22 members, respectively. Five C-type isoforms (αc1, αc2, γc3, γc4, and γc5) are constitutively expressed, whereas others are stochastically expressed in each cell (*6*, *7*). Simple combination statistics lead to an estimated total of 3×10^{10} possible variations for each neuron, making Pcdh isoforms a good candidate for the characterization of neuronal individuality (*8*). At the protein level, it is thought that Pcdhs form tetramers (dimers of dimers) that are formed by either cis or trans interactions. Cis dimers are either homodimers or heterodimers. Trans interactions are mediated by Pcdh homophilic interactions (*9, 10*).

The olfactory system is a good model for studying neuronal individuality. Animals sense and distinguish many different odors. In the mouse, single olfactory sensory neurons express a single odorant receptor (*11*) out of a repertoire of more than 1000 odorant receptors. These neurons project to the olfactory bulb in the brain, forming structures called glomeruli. Through single-cell RNA sequencing, Mountoufaris *et al.* determined that distinct combinations of Pcdhα, -β, and -γ isoforms are expressed in individual mature olfactory sensory neurons, but that expression of C-type isoforms is suppressed. Mice engineered to lack the *Pcdh*α cluster showed somewhat less compact protoglomeruli (glomeruli of newborns) compared to normal animals, whereas mice lacking either *Pcdh*β or *Pcdh*γ showed almost no phenotypic changes. By contrast, mice lacking all three *Pcdh* gene clusters failed to form normal protoglomeruli. Moreover, individual olfactory sensory neurons did not display the normal "cup"-shaped axonal arbors, but exhibited a heavily clumped and distorted appearance, indicative of the loss of self-avoidance. To abolish Pcdh diversity in olfactory sensory neurons, the authors

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