# Trace gas emissions and species-dependent ecosystem services

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**The concept of ecosystem services has both potential and peril for conservation biologists. Where these services depend on species-specific processes, the pragmatic nature of the argument has great potential to influence the public and policy makers. However, where these services depend on processes common to many taxa, then the link to preservation of biodiversity is weaker. We discuss one biological process, the emission of volatile organic compounds from plants to the atmosphere, that is highly species-specific and that has important impacts on air quality. We also suggest some research priorities involving phytogenic volatile organic compound emissions.**

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The warmth of ecological feeling for species preservation and for the maintenance of diversity stems, in many cases, from a complex mix of aesthetic, ethical, and even religious convictions. Of the rationalizations presented for the preservation of particular species, the strongest are perhaps those that are derived from the joint consideration of these convictions.

The preservation of species diversity often depends on gaining popular support from non-ecologists. In many instances, ecologists attempt to alert the public to the importance of species diversity and of preserving ecosystems on the basis of practical issues of health and human welfare. Unfortunately, some of these popular utilitarian arguments are subject to severe criticism.

For example, one common argument for the preservation of ecosystems is that they provide 'ecosystem services' [1]. Services refers to processes such as maintaining the level of oxygen in the atmosphere so that animal, and particularly human, life can continue, removing organic material from water so that the water is potable and tasteless, maintaining soil quality, and so on. The activities that result in these services include photosynthesis, respiration and transpiration.

Unfortunately, some service arguments do not necessarily have any implications for the preservation of species diversity, and can be almost independent of species composition. It is therefore difficult to use such ecosystem services as arguments for the preservation of biological diversity, because even ecosystems that have been seriously degraded from the standpoint of species diversity continue to perform most of them. For example, photosynthesis and respiration occur in sewage outlet pools and transpiration occurs in weed beds.

If, as many data suggest, ecosystem-scale processes, such as net carbon (C) and energy exchange, depend primarily upon tree stand age and growth form, rather than on the details of species composition [2], it might be hard to use these services as arguments for the preservation of unmanaged ecosystems. It might well be that, within our measurement abilities, a tree is a tree is a tree, and it matters little whether that tree is within the matrix of a pristine forest or is one of one million clones in a poplar *Populus* spp. plantation. If, in fact, heavily managed and manipulated systems are able to perform services better than are unmanaged ones, then the argument of 'conservation for the preservation of ecosystem services' might be antithetical to the ultimate aims of many conservation biologists. For example, if a rapidly growing forest plantation sequesters more C than does an old-growth forest, then, as long the original forest and the plantation are used in functions that lead to long-term C storage, such as lumber for construction, the plantation provides more than does the forest in terms of this particular service. The crucial, complex question is: 'Are extensive variables, such as Net Primary Productivity, Gross Energy Flux, or Total Biomass (*cf.* [3]) measured over the scale of an ecosystem sufficient for conservation management decisions, or is there need for more detailed information about species-specific processes?' Data are now being collected that could lead to the beginnings of an answer [4].

In the face of such complexity, it might seem tempting to abandon the notion of ecosystem services and to stick with the more familiar terms of 'conservation for the sake of species and habitat preservation'. However, the ecosystem services argument has great potential to appeal to policy-minded administrators and politicians, because these services often impact on society in ways that are relatively easy to quantify in monetary terms [5]. For example, the benefit of water purification by wetlands can be quantified as equal to the money that would have to be spent on a purification plant in the absence of the wetland, or as the cost of the resulting disease or fisheries loss if the water were to pass untreated.

A goal for conservation biologists should be to identify ecosystem services that are highly species specific, so that conservation of species and habitats can be justified in service terms. Here, we introduce one category of ecosystem service that is highly species specific and that is greatly affected by changes in land use: the production and emission by plants of volatile organic compounds (VOCs), which regulate crucial features of atmospheric

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chemistry [6,7]. Plant emission of VOCs is vital in maintaining the redox potential of the atmosphere and air quality, and these emissions also highly species specific. VOC emissions are, therefore, important candidates for consideration by conservationists who wish to argue that individual species provide services that are crucial for human well being, and that biological diversity and integrity must be maintained to help preserve those services.

**Biology of VOCs**

VOCs are organic molecules that have a low enough boiling point that they change from the liquid to the gas phase at a high rate at physiologically realistic temperatures (10–45°C). Once these molecules are in the gas phase, they can diffuse rapidly from the plant to the atmosphere. Plants produce ~$10^{15}$ g VOC $y^{-1}$, and this constitutes ~80% of the chemically reactive VOCs that are added to the atmosphere each year, with most of the remainder coming from fossil fuel combustion [8]. Although some previous research has considered VOCs as pollutants, they do play a vital role in the atmospheric system by serving as the primary determinants of the oxidative capacity of the troposphere (a measure of the potential of the atmosphere to remove pollutant chemicals), the dynamics of carbon monoxide (CO) and tropospheric ozone, and the abundance of atmospheric aerosols [9]. When atmospheric levels of nitric oxide (NO) and $NO_2$ (collectively, $NO_x$) are low, oxidation of VOCs removes ozone from the troposphere. When $NO_x$ levels are high, as occurs in air contaminated by fossil fuel combustion, VOC oxidation increases ozone levels [10].

Another crucial service provided by the larger molecular weight VOCs (those with >9 C atoms) is that they can serve as the organic C in the formation of organic nitrates [25], which can then be removed in precipitation events. The VOCs thus help to remove reactive $NO_x$ from the lower atmosphere. Recent modeling research suggests that monoterpenes, (10-C VOCs) might provide thermal insulation at night in arid ecosystems, thus minimizing the occurrence of low nighttime temperatures that can limit plant growth [11]. Because these VOCs are produced and consumed through complex physiological processes, their rate of emission to the atmosphere is highly sensitive to changing environmental conditions, such as temperature, precipitation, and land use practice.

Most importantly from the perspective of conservation biology, VOC production and emission shows a high degree of species specificity [12]. Certain species produce large quantities of VOCs, whereas others produce only trace amounts. Changes in plant community composition can affect VOC emissions to an extent that swamps all other sources of environmental variation combined. For example, the loss of American chestnut *Castanea dentata* from forests of the eastern USA and the corresponding increase in oak *Quercus* spp. biomass led to an approximate doubling of phytogenic VOC emissions from these forests [13]. However, current changes involving fire suppression and the spread of sugar maple *Acer rubra* (a low emitter) at the expense of oak (a high emitter) will lead to a decline in emissions. Several recent papers have presented the results of surveys of VOC emissions and the construction of emission inventories [14]. We can now begin to make some preliminary estimates of how land-use change in both temperate and tropical regions is likely to affect the impact that plants have on atmospheric chemistry.

The most important changes are likely to be in tropical ecosystems for two reasons. First, VOC emissions show a strong dependency on light and temperature, with a linear response to light and an exponential temperature response across a physiologically realistic range. The high temperature and/or light conditions that are common to many tropical ecosystems, combined with the large number of VOC-emitting species, results in tropical forests contributing >50% of total global VOC emissions [8]. Second, these ecosystems are changing in both species composition and life form at a faster rate than is any other ecosystem type [15]. These changes often involve drastic shifts in the ratio of emitting to non-emitting taxa.

When tropical forests are converted to pasture, the change in species composition (as well as life form) from trees to C4 grasses leads to enormous changes in the flux of VOCs. Although approximately one-third of the tree taxa examined in both tropical Africa and America emit large quantities of isoprene ($C_5H_8$), no C4 grasses have been found to be major emitters (http://www.es.lancs.ac.uk/cnhgroup/iso-emissions.pdf). In fact, the only clade of grasses in which isoprene emission has been frequently found is bamboo [16]. In spite of this lack of isoprene emission, VOCs are produced in grasslands, but they tend to be oxygenated compounds, such as acetone and hexenal, which quickly dissolve in water and are deposited by rain rather than reacting in the gas phase and producing CO and changing ozone dynamics [17].

In contrast to the forest–pasture conversion, the conversion of unmanaged forest to forest plantation often increases the emission rate of VOCs, because many of the common tree species used in forest plantations worldwide, for example *Eucalyptus* and *Populus*, are large emitters of isoprene with emission rates of up to 100 nm $m^{-2}$ $s^{-1}$ [16,18]. Changing the forest from one in which only approximately one-third of the biomass is emitting isoprene to one where all trees are emitters increases emission proportionately. When such plantations occur on large spatial scales, the impacts on atmospheric chemistry can be marked [19].

Although forest conversion to pasture or forest plantation leads to easily predictable changes in

VOC emissions, the changes in species compositions associated with the growth and development of secondary forests do not. For example, one dominant taxon of secondary forests in the New World tropics is *Cecropia*, a genus in which VOC emission has not been found [10,20]. However, many aggrading forests contain large numbers of palms, a group that has some of the highest rates of emission (up to 120 nmol $m^{-2}$ $s^{-1}$ [10,20]. Similarly, data from tropical Africa and America suggest that approximately one-third of successional taxa are major VOC emitters [21,22].

In temperate ecosystems, two of the most important land-use changes that directly affect VOC emissions are the conversion of unmanaged forest to forest plantations and the aggradation of deciduous forests through the shifting of agriculture from the eastern to the western USA [15]. Both of these changes have impacts that are similar to the impacts of similar changes in the tropics. In temperate ecosystems, one of the most important current changes is the expansion of *Populus* plantations for both pulpwood and, with recent advances in wood-processing technology, for lumber. *Populus* has one of the highest VOC emission rates measured to date (commonly up to 80 nmol $m^{-2}$ $s^{-1}$, and the development of *Populus* plantations could have large impacts on the regional air chemistry in areas, such as the Pacific Northwest, that have native forests with low levels of emission. By contrast, as the northeastern USA has become less agicultural, deciduous forests have, to large extent, returned. With their high abundance of *Quercus* spp., these forests have high levels of emission in contrast to the low levels of emission of crop plants (>60 nmol $m^{-2}$ $s^{-1}$ versus <5 $m^{-2}$ $s^{-1}$) [13].

Other large-scale phenomena that might affect global patterns of VOC emissions are shifts in forest distributions in response to climate change. As the climate warms, latitudinal treelines will shift northward, and altitudinal treelines will shift upward. Because two of the most abundant boreal and high elevation taxa, *Populus* and spruce *Picea* spp., are high VOC emitters [23], these changes are likely to cause large increases in VOC emissions in both North America and Eurasia. If such changes are accompanied by extensions of human activity and fossil fuel combustion in these regions (with its concomitant production of NO), then global-scale production of tropospheric ozone is likely to increase [6].

In spite of the uncertainties associated with specific land-use changes, several statements regarding land-use change and the impacts of vegetation on atmospheric processes can be made. First, and most importantly, the notion of species-specific impacts on ecosystem services is extremely applicable to the question of VOC emission from ecosystems. Unlike ecological processes, such as photosynthesis and respiration, which are common to all plant species and which do not often vary more than threefold among species, VOC emission from plants varies by up to four orders of magnitude. For example, oak and maple maximum photosynthetic rates differ by only ~50%, whereas their VOC emission rates differ by four orders of magnitude or more [13]. Conservation efforts should therefore consider VOC emissions when trying to calculate the effects of a land-use change on the service an ecosystem provides.

In addition, because so few agricultural species are high emitters of VOCs, any changes associated with the conversion of unmanaged forests to agricultural uses will tend to decrease VOC emissions. Also, in areas where agriculture is declining and fallow lands are returning to forest, the VOC flux will increase, both because of the increase in biomass associated with forest aggradation and the increase in the proportion of biomass that comprises high-emitting species. Finally, the conversion of unmanaged forest to forest plantation often involves a dramatic increase in the proportion of VOC-emitting taxa, particularly *Populus* (temperate) and *Eucalyptus* (tropical) and hence in the VOCs emitted from these regions.

These changes in VOC emission patterns are likely to have profound and context-dependent effects on regional and continental air chemistry. If agricultural extensification occurs at the expense of native forest, the emission of VOCs to the atmosphere will decline. If this occurs in a low-$NO_x$ environment, ozone concentrations might rise. If, however, it occurs in high-$NO_x$ air, then ozone concentrations will decrease [24]. Correspondingly, as agricultural land returns to forest, the increase of VOC emissions into air with low levels of reactive N-containing compounds will both decrease ozone levels and help to reduce further the concentrations of reactive N by producing organic nitrates. Forest plantations are a unique type of agriculture, because they tend to lead to a net increase in VOC emissions.

## Future efforts

Future research efforts on the conservation implications of VOC emissions should focus on four main areas. First, and most importantly, as scientists examine ecosystem services, they should focus on the implications of land-use and habitat change on VOC emission from vegetation and how these changes might alter air chemistry, in particular, the dynamics of ozone and hydroxyl radicals. Second, of the major biome types currently undergoing the largest changes in relative extent, grasslands have received disproportionately little study with regard to their VOC emissions; a gap that must be filled through further research. Third, although many important conservation efforts are occurring in Asia, very little is known about VOC emissions from these ecosystems, although many of them are experiencing rapid change. Therefore, efforts to examine VOCs from Asian ecosystems are extremely important. Lastly, vegetative canopies can serve as sinks as well as sources of reactive trace gases. The influence of species composition on canopy sink strength has received little attention but could play a major role in biosphere–atmosphere interactions.

At the very least, evaluation of VOCs from diverse circumstances and locations will improve our ability to make a realistic evaluation of the role of particular species in the provision of services. This overall evaluation is difficult, because their significance is context dependent, for example, whether the VOCs are being emitted into an atmosphere with a low or high reactive N concentration. The spatial scale of VOC emission studies, the forest stand, is similar to the scale at which property is often held and land-use decisions made. In addition, the temporal scale of VOC impacts on the atmosphere is short enough that these impacts can easily be accounted for by policymakers. These similarities of scale make VOC emissions ideal processes to be incorporated into evaluations of ecosystem services. The species-specific nature of these emissions makes them useful to consider by those wishing to conserve biological diversity.

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## Articles of interest

Articles of ecological or evolutionary interest in recent issues of other *Trends* and *Current Opinion* journals

**Where will the wood come from? Plantation forests and the role of biotechnology.** Trevor M. Fenning and Jonathan Gershenzon *Trends in Biotechnology*, 2002, 10.1016/S0167-7799(02)01983–2

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