REVIEW

Ecosystem service provision by road verges

Benjamin B. Phillips | James M. Bullock | Juliet L. Osborne | Kevin J. Gaston

1Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, UK
2NERC Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK

Correspondence
Benjamin B. Phillips
Email: b.b.phillips@exeter.ac.uk

Funding information
Natural Environment Research Council, Grant/Award Number: NE/L002434/1; Cornwall Area of Outstanding Natural Beauty; National Capability, Grant/Award Number: NEC06895

Handling Editor: Peter Manning

Abstract

1. Roads form a vast, rapidly growing global network that has diverse, detrimental ecological impacts. However, the habitats that border roads ('road verges') form a parallel network that might help mitigate these impacts and provide additional benefits (ecosystem services; ES).

2. We evaluate the capacity of road verges to provide ES by reviewing existing research and considering their relevant characteristics: area, connectivity, shape, and contextual ES supply and demand. We consider the present situation, and how this is likely to change based on future projections for growth in road extent, traffic densities and urban populations.

3. Road verges not only provide a wide range of ES, including biodiversity provision, regulating services (e.g. air and water filtration) and cultural services (e.g. health and aesthetic benefits by providing access to nature) but also displace other habitats and provide ecosystem disservices (e.g. plant allergens and damage to infrastructure). Globally, road verges may currently cover 270,000 km² and store 0.015 Gt C/year, which will further increase with 70% projected growth in the global road network.

4. Road verges are well placed to mitigate traffic pollution and address demand for ES in surrounding ES-impoverished landscapes, thereby improving human health and well-being in urban areas, and improving agricultural production and sustainability in farmland. Demand for ES provided by road verges will likely increase due to projected growth in traffic densities and urban populations, though traffic pollution will be reduced by technological advances (e.g. electric vehicles). Road verges form a highly connected network, which may enhance ES provision but facilitate the dispersal of invasive species and increase vehicle–wildlife collisions.

5. Synthesis and applications. Road verges offer a significant opportunity to mitigate the negative ecological effects of roads and to address demand for ecosystem services (ES) in urban and agricultural landscapes. Their capacity to provide ES might be enhanced considerably if they were strategically designed and managed for environmental outcomes, namely by optimizing the selection, position and management of plant species and habitats. Specific opportunities include reducing mowing frequencies and planting trees in large verges. Road verge management for ES must consider safety guidelines, financial costs and ecosystem disservices, but is likely to provide long-term financial returns if environmental benefits are considered.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. Journal of Applied Ecology published by John Wiley & Sons Ltd on behalf of British Ecological Society.
1 | INTRODUCTION

Roads form a vast global network and are a ubiquitous and fundamental component of human-dominated landscapes. They have diverse and often profound negative ecological impacts, primarily habitat loss and fragmentation, light and noise pollution, chemical pollution of air and water, and the direct mortality of wildlife due to collisions with vehicles (Forman et al., 2003). These negative impacts affect surrounding landscapes, often up to distances of 1 km, so potentially impacting 20% of all land (Ibisch et al., 2016). However, given how central roads are to the global economy and to everyday life, it is more realistic to look to reduce and mitigate these negative impacts, and to develop opportunities for positive environmental contributions, rather than simply seek to remove the source of the problems altogether.

‘Road verges’ provide one such set of opportunities. They are the strips of land (known by a variety of terms) in the immediate vicinity of roads that separate them from the surrounding landscape (Figure 1). Road verges tend foremost to be written about in the context of more heavily ‘constructed’ roads. But the concept, and our definition here, extends much more widely as virtually all roads have associated bordering strips of land that are distinctively different, and typically much more heavily and anthropogenically disturbed, from that which lies beyond (Figure 1). Road verges are commonly grassland habitats, but can be shrubland, forest or artificial arrangements of

**FIGURE 1** Road verges and the wide variety of forms that they can take: (a) grassy road verges along the D2 highway in the Czech Republic, (b) road verges with grass, shrubs and trees along a busy expressway near Kuala Lumpur, Malaysia, (c) regularly mown, grassy road verges in a suburban area in Sheffield, UK, (d) a tree-lined urban street in Chittagong, Bangladesh, (e) road verges separating surrounding forest in Northwest Territories, Canada, (f) wide, grassy road verges that have been managed by cutting in Namibia, (g) a small lane with narrow road verges that form vertical habitats with adjacent hedges in Devon, UK and (h) a dirt road in the Namib Desert, Namibia, where the only apparent road verge has been created by vehicles pulling over. Photographs by Kevin J Gaston (c, e, f, h), Ruth Saunders/Dittiscombe (g) and from Wikimedia Commons ((a) by RomanM82 and (b) by mailer_diaibo, both licensed under CC BY-SA 3.0, and (d) by Moheen Reeyad, licensed under CC BY SA 4.0)
trees and horticultural plants (Figure 1), and we use the term also to include bare earth and freshwater bodies (e.g. ditches). On a global scale, verges are hugely variable and can range from a few centimetres of disturbed road edge, to a few metres of regularly mown vegetation, to many metres of unmanaged habitat (Figure 1). Road verges can support biodiversity and there is growing appreciation of their potential value as a conservation resource (Gardiner, Riley, Bommarco, & Öckinger, 2018). This paper goes one step further by proposing that road verges and the species they support have the capacity to provide ecosystem services (ES) on a large scale.

Road verges serve a range of purposes: they can increase visibility and improve aesthetics for road users, provide a route for road drainage or a refuge for pedestrians, and buffer people and the surrounding landscape from adverse impacts of traffic. However, the land itself is largely unutilized and is generally only managed for safety purposes—namely cutting, burning or grazing to reduce vegetation height and improve visibility for road users—or not managed at all. There is thus the potential to design and manage road verges in a way that enhances ES. While roads run like a network of veins across landscapes, causing widespread negative ecological impacts to adjacent areas, road verges form a parallel network and have the potential both partially to mitigate negative impacts of roads and to deliver environmental benefits. However, this must be set against the loss of ES from the habitats that road verges displace, as well as potential ecosystem disservices. The potential for road verges to provide ES may be particularly marked because of the spatial extent of road verges, the breadth of positive environmental contributions that they can make and there being little competition for their use. There is also debate around how road verges are managed: whether they should be managed primarily for safety, or also as a component of green and conservation infrastructure (e.g. Plantlife, 2019).

In this paper, we examine the actual and potential contributions of road verges to ES provision. First, we provide a conceptual framework and review the literature to identify the extent of current knowledge and evidence. We then use this as the basis for exploring the characteristics of road verges that might influence their capacity to provide ES including their area, connectivity, shape and contextual ES supply and demand. In each case, we consider the current supply of ES from verges, and then how this is likely to change in the future based on projections for growth in road extent, traffic densities and urban populations. Finally, we provide some key considerations for designing and managing road verges for ES and an agenda for future research. Throughout, our focus is on road verges, but many of the general principles might apply equally to the vegetated borders of other linear transport infrastructure such as railways and canals.

2 | MATERIALS AND METHODS

2.1 | Framework

Across the world, road verges are likely to provide a diverse array of ES that primarily benefit road users (both drivers and pedestrians) and local people (Figure 2). We broadly follow the CICES framework (Haines-Young & Potschin, 2018), whereby ES are the contributions that ecosystems make to human well-being. Road verges are well placed to provide ES for three main reasons: (a) roads and traffic produce environmental pollution of air, water and soils, which regulating ES can mitigate; (b) road verges by definition occur where people live and/or move, providing high demand for ES and (c) road verges generally occur at highest densities in more human-modified landscapes, where there is a low background supply of many types of ES. The potential suite of ES provided by a particular road verge will depend on the characteristics of the verge (e.g. size and habitat type), the road (e.g. amount of traffic), the surrounding landscape (e.g. urban, agricultural or natural), the geographical region, and the behaviours and cultures of local people (e.g. use of raw materials from road verges).

Principally, road verges may provide provisioning ES (e.g. timber and other raw materials), fundamental regulating ES (e.g. global and local climate regulation), more contextual regulating ES (e.g. supporting populations of plants and/or animals that provide crop pollination, pest control and nutrient cycling, and, due to their proximity to roads, filtration of air and water) and cultural services (e.g. health and aesthetic benefits by providing access to nature; Figure 2). However, road verges likely also provide ecosystem disservices (Figure 2), and the net benefits need to be compared with the loss of ES from the habitats that road verges have displaced.

2.2 | Literature search

We carried out a formal literature search using Web of Science to identify scientific publications (up to 1 June 2019) addressing ES provision by road verges. This literature is varied and covers a broad range of subjects. Thus, we aimed for a comprehensive, but not necessarily complete review. We used a search string to identify studies on road verges (covering names and forms that road verges take across the world), combined with the phrase ‘ecosystem service’ or one of 13 search strings relating to the main ES that road verges might provide (see Appendix S1). We screened the search results using titles and abstracts, or where necessary, the main text. Relevant studies were those that measured or inferred ES provision from road verges or similar roadside areas. When a recent literature review was available for an ES, we did not retrieve empirical studies. The key details and findings of relevant studies were recorded in a spreadsheet (Appendix S1).

3 | EVIDENCE FOR ES PROVISION

So far, research on road verges has primarily focused on (a) a few ES (primarily biodiversity provision, air filtration and water filtration), studied in isolation; (b) a few contexts (primarily urban environments (reviewed in O’Sullivan, Holt, Warren, & Evans, 2017; Säumel, Weber, & Kowarik, 2016) and the ES provided by urban trees [reviewed in Salmond et al., 2016]); and (c) a few geographical regions (primarily in Europe, North
America and Asia; Appendix S1). Furthermore, few studies compare ES provision by road verges to that from the habitats they have displaced, especially in natural landscapes (probably resulting from the geographical limit of the studies), making it difficult to assess the net impact of road verge construction. Rather than focusing our review on these limited contexts, we provide a holistic framework for ES provision by road verges in all contexts, on a global scale, and use this as the basis for exploring the current and future potential of road verges for ES provision. We direct readers to recent reviews where available, or otherwise describe some of the most relevant empirical studies. We provide the full list of studies in Appendix S1.

3.1 | Biodiversity

Road verges support populations of some plants and animals (reviewed in Gardiner et al., 2018). For example, road verges enhance the distribution and dispersal of many plant species (reviewed in Lázaro-Lobo & Ervin, 2019), often supporting a greater diversity and abundance of plant species than various adjacent habitat types—possibly because they receive more (locally produced or dispersed) seeds (reviewed in Suárez-Esteban, Fahrig, Delibes, & Fedriani, 2016). Verges also have a similar diversity and greater abundance of insects than comparable habitats such as grasslands (reviewed in Villemey et al., 2018), and provide important nesting and foraging habitats for birds (reviewed in Morelli, Beim, Jerzak, Jones, & Tryjanowski, 2014).

3.2 | Carbon sequestration and storage

Road verge soils and vegetation can provide a substantial carbon sink. A study in the United States found that roadside filter strips had similar carbon storage and sequestration to grasslands (Bouchard, Osmond, Winston, & Hunt, 2013). Urban roadsides can provide even greater carbon stocks: urban soils have 3–5 times greater carbon stocks than natural soils (because anthropogenic processes provide carbon sources and the upward growth of soil over long periods, resulting in both faster and deeper carbon accumulation), of which urban roadsides have some
of the greatest stocks of black carbon (produced from burning fossil fuels; reviewed in Vasenev & Kuzyakov, 2018). Studies in Brazil estimated that afforestation of highway road verges could result in the sequestration of up to 218 tonnes of CO₂/ha of road verge over a 10-year period, equivalent to 655 tonnes of CO₂/km of highway (Da Silva, Braga Alves, & Alves, 2010), with an estimated carbon sequestration of 55.3 million tonnes across all of Brazil, which represents US$26.5 billion in the carbon market (Fernandes et al., 2018).

### 3.3 Regulation of air, water, soil and associated pollution

Many studies have shown that roadside vegetation can substantially improve air quality, but vegetation must complement street geometry otherwise it can have the opposite effect, for example, tall trees improve air quality along open roads but reduce air quality when roads are bordered by tall buildings (‘street canyons’) because they trap pollutants (reviewed in Abhijith et al., 2017; Baldauf, 2017; Gallagher et al., 2015; Janhäll, 2015). Studies consistently show that roadside vegetation can reduce noise levels by 2–10 dB, depending on the type, amount and arrangement of vegetation (Appendix S1). For example, one study found that road verges with trees and shrubs doubled the rate of noise reduction over 20 m compared with those with minimal vegetation (Ow & Ghosh, 2017). Tall roadside vegetation, particularly street trees, is important for maintaining a comfortable microclimate, especially in hot countries, with studies showing temperature reductions of several degrees Celsius (Appendix S1). Road verges can provide a barrier to soil erosion: one study found that the addition of a 90 cm wide grass strip at the edge of forest roads reduced total sediment loss by an average of 56% (Appelboom, Chescheir, Skaggs, & Hesterberg, 2002). Many studies demonstrate that roadside vegetation, filter strips and swales (shallow, vegetated channels) provide water filtration, bioremediation and flow regulation (Appendix S1), for example reducing water flow by 75%–90% during storm events (Henderson, Smith, & Fitch, 2016), and swales reducing total suspended soils by 56% and trace metals by 62% (reviewed in Fardel, Peyneau, Béchet, Lakel, & Rodríguez, 2019).

### 3.4 Pollination and pest control

Many studies in Europe and North America demonstrate that road verges are important semi-natural habitats for insect pollinators (reviewed in Hopwood et al., 2015) and natural enemies of pests (Appendix S1), which are known to spill over from areas of high-density into surrounding landscapes (reviewed in Blitzer et al., 2012). However, few studies have tried to measure spill-over from road verges, or the resulting impact on pollination or pest control services. Three studies provide some evidence: length of road verge in the surrounding landscape was positively related to the activity density of predatory spiders in oilseed rape fields in two studies in Austria (Drapela, Frank, Heer, Moser, & Zaller, 2011; Drapela, Moser, Zaller, & Frank, 2008) and to parasitism of a caterpillar pest in cabbage fields in a study in the Netherlands (Bianchi, Goedhart, & Baveco, 2008).

### 3.5 Cultural services

Road verges can deliver a number of cultural ES. For example, the addition and strategic management of vegetation along roadsides can improve aesthetics for pedestrians and road users (reviewed in Blumentrath & Tveit, 2014), increase nearby property values, reduce driver stress, and provide health benefits to local people by improving access to nature (reviewed in Lucey & Barton, 2012; O’Sullivan et al., 2017; Säumel et al., 2016).

### 3.6 Ecosystem disservices

Nature in road verges can also have negative consequences for people. For example, plants can reduce air quality, produce allergens, and damage and disrupt infrastructure (e.g. falling trees, tree roots and leaf fall), and there can be negative social perceptions of infrequent management as neglect (Säumel et al., 2016). However, these effects have received much less attention in the literature than have the ES provided by road verges.

### 3.7 Large-scale ES multi-functionality

Currently, there are few empirical studies on road verges that consider multiple ES or ES provision beyond the local scale (Appendix S1). However, the overall potential of road verges for ES provision is also determined by their broader-scale characteristics, namely their extent, their impact on connectivity, and the supply of and demand for ES in the surrounding landscape. In the following sections, we discuss the current situation and future projections relating to these characteristics to explore the potential of road verges for providing ES.

### 4 Global extent of road verges

The global road network is estimated to be 36 million km in length (Central Intelligence Agency, 2017). Most of this network is bordered by road verges in some form (Figure 3), with estimated areas of 2,400 km² (1% of land) in Great Britain (Plantlife, 2013) and 48,500 km² (0.5% of land) in the United States (Forman et al., 2003), assuming average verge widths of 4 and 3 m, respectively. Assuming a similar area of road verge per length of road in the rest of the world, there may well be 270,000 km² of road verge globally (0.2% of land), which is similar to the total area of the United Kingdom. The ES provided by road verges is therefore significant if only due to the vast area that they collectively cover. For example, if the average carbon sequestration of road verges is similar to an...
FIGURE 3  The spatial extent of road verges is illustrated by the high density of roads in a small area of the United Kingdom, and by the ubiquity of road verges in a 36 km² subarea (near Truro, Cornwall; 50.2759N, −5.1586E). In the map, road verges include areas of grassland, scrub and trees, but exclude roadside hedges. The histogram of road verge widths shows that the size and shape of road verges varies dramatically: most road verges in this area are less than 2 m wide, but a number of road verges are between 20 and 75 m wide, which may affect their capacity to provide particular ES, and resulting management approaches and priorities. Maps and data were produced by drawing polygons around road verges using satellite imagery from Google Earth and verifying using Google Street View (Google, 2019), then importing to ArcMap 10.5.1 (ESRI, 2017). Road verge widths were calculated by creating centrelines for each road verge, converting them to points at 5 m intervals, measuring the distance from each point to the nearest road verge edge, then multiplying by 2.

|                        |            |
|------------------------|------------|
| Area of grid           | 36.00 km²  |
| Length of roads:       | 129.98 km  |
| Area of road verges:   | 0.36 km² (36 ha) |
| % of land covered by road verges: | 1.01% of land |
| Area of road verge per km road: | 2,787.34 m² |
average value for grasslands (0.054 kg C m\(^{-2}\) year\(^{-1}\); reviewed in Conant, Paustian, & Elliott, 2001), which is probably a conservative estimate (Bouchard et al., 2013; Vasenev & Kuzyakov, 2018), then they may sequester 0.015 Gt C/year globally—nearly 1% of the annual carbon sink provided by the world's 4 million km\(^2\) of forests (Pan et al., 2011).

4.1 | Future developments in extent of verges

The global road network is predicted to expand by a further 25 million km by 2050 (a 70% increase in length), with the largest increases occurring in China and India (International Energy Agency, 2013). Road and road verge construction will displace habitats and cause many negative ecological and social impacts, but there will also be the opportunity to design and manage road verges explicitly to help mitigate these impacts. The net change in ES provision from road verge construction will depend on the habitat being replaced. In countries with growing populations and high quantities of natural habitats remaining, road verges will often replace habitats with high biodiversity and ES value such as forests (Ibisch et al., 2016; Laurance et al., 2014)—a significant net loss of ES. In Europe and North America, road verges will more often replace farmland because this is the most common habitat type (European Commission, 2018). Although newly constructed roads will cause major negative ecological and social impacts (e.g. pollution), newly constructed road verges could provide net gains in ES under some circumstances. For example, conversion of arable farmland to grassland increases soil organic carbon by an average of 18% (reviewed in Kämpf, Hözel, Störrle, Broll, & Kiehl, 2016) and the establishment of vegetated strips around agricultural fields benefits biodiversity, reduces nutrient, soil and water loss (reviewed in Haddaway et al., 2018), though obviously reduces crop provisioning. However, the ES from road verges will very rarely outweigh the negative environmental impacts of roads, so road construction should principally aim to minimize environmental impacts (Laurance et al., 2014) and only consider road verges as a tool for partially mitigating and offsetting them.

5 | DEMAND FOR ES ALONG ROADS AND IN ADJACENT LANDSCAPES

The landscapes in which roads occur can broadly be classified as urban or rural. In Britain, 38% of roads occur in urban areas and 62% in rural areas (Department for Transport, 2018a), while in the United States just 21% of roads occur in urban areas and 79% in rural areas (Forman et al., 2003). These two land-use types give rise to demand for different suites of ES (Figure 2). Urban areas are defined by high densities of people and currently hold 55% of the global population, though numbers are as high as 82% in North America and 74% in Europe (United Nations, 2018). ES required in urban areas include those that improve human health and well-being, reduce pollution (e.g. through air filtration and noise reduction) and regulate environmental conditions (e.g. local temperature; Gómez-Baggethun & Barton, 2013; Figure 2). Rural areas are often dominated by agriculture, which gives rise to demands for ES that improve agricultural production (e.g. maintaining soil health and providing crop pollination) and sustainability (e.g. reducing soil erosion and flooding), or otherwise by natural and semi-natural habitats, which give rise to demands for ES that mitigate environmental pollution (Figure 2). In both urban and agricultural landscapes, there are often few other high-quality habitats, so measures to increase both biodiversity and ES are especially important, and in all cases there will be demand for ES that minimize negative impacts of roads.

The extent of demand for ES that mitigate pollution and benefit road users will be affected by the traffic density of a particular road and the proximity and density of people, dwellings and natural resources. In Britain, major roads constitute just 13% (50,500 km) of roads but carry 66% of road traffic (Department for Transport, 2018a). In the United States, the interstate highway network comprises just 1.2% of roads, but carries 22.8% of traffic (Forman et al., 2003). The majority of the demand for pollution-mitigating ES is therefore associated with these heavily used roads, which are also likely to have the widest road verges (Figure 3). Proximity to the pollution source is one of the most important factors determining the effectiveness of pollution-mitigation measures (e.g. Janhäll, 2015), so road verges are well positioned for this purpose. Given that a minority of roads support a majority of traffic, focusing efforts on improving road verges next to heavily used roads (e.g. through strategic habitat creation, tree planting or improved mowing regimes) will provide disproportionate improvements in ES provision.

5.1 | Future developments in ES demand from verges

ES provision by road verges will become more important as human populations increase, urbanization continues and surrounding habitats are further degraded. By 2050, the proportion of the global population living in urban areas is projected to increase from 55% to 68%—an estimated 2.5 billion additional urban residents (United Nations, 2018). This will dramatically increase pressures to use urban and peri-urban land to benefit the health and quality of life of urban residents, with road verges offering a major opportunity for doing so.

Although the total length of road is predicted to remain relatively stable in many regions with already well-developed networks (e.g. Europe and North America; International Energy Agency, 2013), traffic densities are still expected to increase. In Britain, the total distance driven on roads was 530 billion km in 2017—an increase of 8% over the previous 5 years—with similar increases across all road types (Department for Transport, 2018b). Rising traffic densities will increase the demand for pollution-mitigating ES along existing roads, though vehicle emissions will reduce in the long term. In Britain, CO\(_2\) emissions
from road transport decreased by 4% between 2000 and 2015, with similar decreases in NO$_x$ and particulate matter (despite a 9.3% increase in vehicle miles), largely due to improvements in fuel efficiency and the uptake of ultra-low emission vehicles (Department for Transport, 2018b). Reductions in road transport emissions will be further accelerated by the phasing out of diesel vehicles and uptake of electric vehicles, which suggests an overall reduction in demand for ES that mitigate road and traffic pollution in many European countries. However, road traffic and associated pollution will increase in countries such as India and China due to the expansion of road networks (International Energy Agency, 2013), growing populations and rising GDP.

**6 | ROAD VERGES AS NETWORKS**

Roads cause habitat fragmentation and can be a major barrier to movement for many species (reviewed in Forman et al., 2003), though some species benefit (Bullock et al., 2018). While fragmentation can negatively affect ES supply, it may improve flows of ES to people and subsequent ES provision (Mitchell et al., 2015). As described in the previous section, this is especially true for road verges because they permeate urban and agricultural landscapes, in which there is high demand for certain ES. In addition, road verges form a network of habitats that may facilitate the movement and dispersal of species and therefore affect ES provision. Connectivity will benefit ES provision if road verges act as corridors for ES-providing species (e.g. pollinators and natural enemies), or if their connectivity results in greater overall biodiversity in the road network and connected patches (Mitchell, Bennett, & González, 2013; Schwarz et al., 2017). There are no empirical studies testing how connectivity affects ES provision in road verges, though some indirect evidence for benefits. For example, greater connectivity increases pollinator diversity (Holzschuh, Steffan-Dewenter, & Tscharntke, 2010) and facilitates pollinator movement (Cramer, McCollin, & Ollerton, 2012), which can increase pollination (Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008; Townsend & Levey, 2005). However, road verges are likely to be unsuitable as corridors for many species (e.g. Oprea, Mendes, Vieira, & Ditchfield, 2009) and their role as corridors will be highly dependent on the quality of the surrounding habitat matrix. Furthermore, road verge corridors will provide ecosystem disservices if they increase vehicle–wildlife collisions, especially with large mammals, which can cause damage to vehicles and risk to human life. Road verge corridors may also facilitate the distribution and dispersal of invasive species (e.g. exotic plants; reviewed in Lázaro-Lobo & Ervin, 2019), which may degrade ES (reviewed in Vilà & Hulme, 2017). For example, in South Africa, road verges are a major conduit for the spread of invasive plant species, which are now estimated to cover 10% of the country and have negatively affected biodiversity and water security, intensified the impact of fires and increased soil erosion, and as such have required large-scale and costly management such as by the Working for Water programme (Department of Water Affairs, 2018).

**6.1 | Future developments in connectivity provided by verges**

Projected increases in the extent of the global road network will further fragment habitats and reduce connectivity in natural landscapes. However, road verges might increase connectivity in highly modified urban and agricultural landscapes if road verges of suitable size, habitat quality and continuity are created alongside roads, at least for species that are highly mobile or able to persist in narrow, linear habitats (e.g. Tremblay & St. Clair, 2009). Strategic design and management of road verges might improve the capacity of many species to use them for movement and dispersal, though limitations to verge size and shape will still make them unsuitable for many. There are a number of national- and international-scale projects that aim to increase habitat connectivity. For example, the B-Lines project by the charity Buglife aims to increase habitat connectivity across the United Kingdom by creating and restoring 1.500 km$^2$ of flower-rich habitat (Buglife, 2019), which will improve the quality of habitats within the road network and beyond. International projects such as the Mesoamerican Biological Corridor in Central America and Natura 2000 in Europe aim to increase large-scale connectivity across landscapes, where roads are primarily considered to be barriers. If road verges were integrated into such projects, they might play an important future role in increasing connectivity between natural and semi-natural habitats, particularly across otherwise habitat-poor, human-dominated landscapes where roads often occur. However, the potential for vehicle–wildlife collisions would need to be assessed and addressed, to reduce risks to both people and wildlife.

**7 | MANAGEMENT FOR ES**

Currently, road verges are largely managed for safety purposes, or are not managed at all. If there was a change towards managing verges for environmental outcomes, their ES provision could probably be increased substantially. Given the global extent of road verges, it is difficult to make specific management recommendations that have general applicability (recommendations have recently been made for managing road verges in urban areas in Europe; reviewed in O’Sullivan et al., 2017; Säumel et al., 2016). Instead, we propose five key considerations for improving ES provision by road verges (Table 1) and three management actions that are potential win–wins—boosting ES provision at little or reduced cost (Box 1). Here, we describe examples of relevant projects.

In the United Kingdom, there is growing support for road verges to be managed for nature conservation outcomes, primarily led by the charity Plantlife (Plantlife, 2019). Plantlife’s campaign aims to improve the timing and frequency of verge cutting to benefit the flowering and seed set of plants, and the phenological cycles of insects. There is strong evidence that strategic management can benefit plant and insect communities, for example mowing once or twice per year reduces the vigour of dominant species, increasing plant...
### TABLE 1 Five management considerations for improving ecosystem services (ES) provision by road verges

| Management consideration | Description | Examples |
|--------------------------|-------------|----------|
| 1. The ES or ES bundle(s) | What is the context of the surrounding landscape and the people that live there? Which ES are needed by those people, and which can be provided by the road verge, given ecological, climatic and social constraints? Broadly, this will be dictated by the road type and surrounding land-use (Figure 2), but local- or region-specific considerations or issues may justify prioritizing specific ES | Surrounding land-use: prioritize ES related to human health and well-being in urban areas, agricultural production and sustainability in agricultural areas, and mitigation of pollution and other negative ecological impacts of roads in natural areas (Figure 2) Road type: prioritize ES related to pollution mitigation on heavily used roads Social considerations: identify social factors that might facilitate or limit peoples' use of ES from road verges, for example, socio-economic status and access to nature may affect health and recreational benefits from road verges Environmental issues: identify climatic issues (e.g. extreme temperatures or flooding) and other environmental issues (e.g. poor air or water quality, soil erosion) that might be addressed by road verges |
| 2. The plant species and habitats | Which species or habitats can best provide the desired ES? Plant species can differ markedly in their capacity to provide ES, for example due to size, leaf surface characteristics, growth rates, and phenology. If the desired ES are delivered by animals, the aim should be to provide plant species or create habitats (through planting or management) that support populations of those animals (e.g. pollinators). Tools that are available to help with such decisions include i-Tree for the United States, Canada, UK, Australia and Mexico (United States Forest Service, 2019), TransPlant for the USA (California Department of Transportation, 2019) and O’Sullivan et al. (2017) for the United Kingdom | Air filtration: affected by the height, thickness, coverage, porosity and density of vegetation, and by plant species characteristics (reviewed in Abhijith et al., 2017; Baldauf, 2017; Janhäll, 2015) Carbon sequestration: four times more carbon stored if road verges are planted with exotic tree species (Eucalyptus spp. and Pinus spp.) instead of native Atlantic rainforest species in Brazil (Da Silva et al., 2010) Erosion control: grass species have different root depths, which affects their ability to reduce erosion in road verges (Brown, Percivalle, Narkiewicz, & DeCuollo, 2010) Noise reduction: coniferous tree species are slightly better at reducing noise than broad-leaved tree species (Nasiri, Agricultural, & Reso, 2015) Pollinators: restored prairie road verge habitats support more pollinators than those dominated by non-native vegetation (Hopwood, 2008) Temperature regulation: tree species differ in their cooling ability (Stratópoulos, Duthweiler, Häberle, & Pauleit, 2018) Water filtration: infiltration system effectiveness is affected by the planted species (Leroy et al., 2017) |
| 3. The spatial arrangement of plants and habitats | The size and shape of a road verge will determine its capacity to provide ES, to support viable populations of species, and to act as a habitat corridor. This will be a major limitation for existing road verges, so future road construction should consider this from the outset, though must also account for the direct loss of habitats and ES due to road verge construction. Regardless of size, strategic spatial arrangement of plants and habitats can enhance road verge ES provision, and poor design may result in disservices. For ES-providing animals (e.g. pollinators and pest natural enemies), locating habitats along the exterior edges of road verges may reduce their exposure to traffic and facilitate their movement to ES beneficiaries in adjacent land (e.g. movement of pollinators to flowering crops). A mosaic approach, whereby different parts or sections of road verge are managed differently or at different times, may also provide multiple habitat requirements for ES-providing animal species or provide a greater range of ES | Size: Increasing the width of farmland grass strips from 2 to 5 m increases their ability to intercept soil sediment from 55% to 84%, nitrogen from 29% to 58% and phosphorus from 23% to 48% (reviewed in Van Vooren et al., 2017). Spatial arrangement: Air filtration: affected by proximity of vegetation to the pollution source and other factors; poor design can reduce air quality, for example, trees in street canyons reduce air flow and concentrate pollutants (reviewed in Abhijith et al., 2017; Baldauf, 2017; Janhäll, 2015) Noise reduction: affected by tree density (Ow & Ghosh, 2017) Pollinators: benefit from mosaic management (e.g. Noordijk et al., 2009) and prioritizing habitats a few meters back from the road edge (Phillips, Gaston, Bullock, & Osborne, 2019) Temperature regulation: affected by vegetation type and configuration (Sodoudi, Zhang, Chi, Müller, & Li, 2018) Water filtration: affected by swale design characteristics (Fardel et al., 2019) |
| 4. Routine management | Routine management of road verges (e.g. cutting regime) may affect ES provision. However, both the financial and environmental costs of management must be considered. For example, management frequency and the machinery required will affect the amount of noise pollution and fossil fuel emissions, and therefore the net benefits of the ES provided (Säumel et al., 2016), though also the demand for mitigating ES | Mowing twice per year and removing hay is optimal for plant diversity (reviewed in Jakobsson et al., 2018) and insect pollinators (Noordijk et al., 2009) Leaving areas uncut reduces water flow and improves water filtration (Henderson et al., 2016) |

(Continues)
Hensgen, & Wachendorf, 2016; Appendix S1), which are often a grass cuttings for biogas production (e.g. Piepenschneider, Bühle, the expense of most other ES. Other studies explore the use of road verge vegetation with a monoculture crop is likely to be at (and free up other areas for nature conservation). But, replacing & Qin, 2015), which might provide a considerable provisioning ES for growing biofuel crops (Voinov, Arodudu, Van Duren, Morales, & Lindborg, 2018), flower species richness, flower abundance and species richness (reviewed in Jakobsson, Bernes, Bullock, Verheyen, & Lindborg, 2018), flower species richness, flower abundance and pollinator abundance (Noordijk, Delille, Schaffers, & Sykora, 2009), which are likely to benefit pollination services and a range of other ES (Schwarz et al., 2017).

It has recently been suggested that road verges could be used for growing biofuel crops (Voinov, Arodudu, Van Duren, Morales, & Qin, 2015), which might provide a considerable provisioning ES (and free up other areas for nature conservation). But, replacing road verge vegetation with a monoculture crop is likely to be at the expense of most other ES. Other studies explore the use of grass cuttings for biogas production (e.g. Piepenschneider, Bühle, Hensgen, & Wachendorf, 2016; Appendix S1), which are often a by-product of routine road verge management. The diversity of plants and insects benefits from cuttings being removed from road verges, which reduces soil nutrients and provides gaps for seedlings (Jakobsson et al., 2018). Currently, cuttings are rarely removed due to the financial costs of collection and disposal but using cuttings for biogas might make their removal financially viable and even profitable. Furthermore, Piepenschneider et al. (2016) found that two cuts per year was optimal for maximizing biomass, which is also optimal for plant species richness (Jakobsson et al., 2018).

There are a growing number of ‘green infrastructure’ projects, which are pioneering the use of public infrastructure to deliver environmental benefits, including using road design and roadside vegetation to address problems of heat islands and water runoff, and produce better places for people to live (Black, Tara, & Pakzad, 2016). For example, the Green Street project in Edmonston, Maryland (USA) used native trees and vegetation in road verges as an effective form of storm management that captures 62% of all rainfall, while also reducing pollution of the nearby river, filtering airborne pollutants and providing shade to decrease the urban heat island effect (Edmonston Maryland Town Council, 2018). In the United Kingdom, Highways England (the government-owned company charged with managing England’s major roads) recently designated £300 million for environmental projects around roads that result in ‘protecting human and environmental health with clear air and water’, ‘thriving wildlife with increasing biodiversity’, ‘reduced levels of noise and light near homes and in the wider countryside’ and a further £100 million for projects that improve air quality (Highways England, 2015). Such investments are strong evidence for a change in perception towards managing roads and road verges for ES and environmental outcomes, beyond transportation purposes.

| Management consideration | Description | Examples |
|--------------------------|-------------|----------|
| 5. Costs, trade-offs and net benefits | Management must consider the net benefits (accounting for costs), not just the improvements in ES provision. This will incorporate financial and environmental costs of establishment and maintenance, trade-offs between ES, ecosystem disservices and safety. Safety is often the most important consideration for road verge management, and there is the potential for major conflicts, especially when roads are sinuous and road verges are narrow because tall herbaceous vegetation or trees may reduce visibility. To be plausible, road verge management must meet safety guidelines. This will often require compromise, such as allowing regular management of an interior strip for safety purposes, to allow the remainder to be managed to optimize ES provision | Ecosystem disservices: Allergens from plants, harm to people, damage to buildings and infrastructure (e.g. from falling trees and tree roots), and negative social perceptions of infrequent management as neglect (Säumel et al., 2016) Trade-offs: Tree species differ in their provision of different ES (biodiversity value, carbon sequestration, removal of particulate matter, flood alleviation, climate resilience) and disservices (production of volatile organic compounds) (O’Sullivan et al., 2017); for example, less water-demanding tree species might perform better under future climate change, but have a poorer cooling ability (Stratópoulos et al., 2018) The use of road verges for biofuel crops will trade-off with most other ES, though use of grass cuttings for biogas production may provide a win–win ES associated with capturing traffic pollution may negatively affect road verge habitats, reducing their capacity to support biodiversity and ES-providing animals (e.g. pollinators), and to provide associated ES (e.g. pollination) |

**BOX 1** Three management actions that are potential opportunities to boost ecosystem services (ES) provision by road verges at little extra cost, or even reduced cost (win–wins).

1. Reduce cutting frequencies in urban verges; leave areas uncut at the back of rural verges: Cost-savings, benefits for biodiversity and likely a wide range of ES.
2. Plant trees at the back of wide road verges: Initial costs, but low management costs and no safety conflicts if trees are sufficiently far from road edges, so may result in long-term cost-savings due to reduced grassland management.
3. Use verge cuttings to generate biogas: Benefits for biodiversity (and potentially other ES), while providing an income and potential profit.
BOX 2 Five priority areas for future research of ecosystem services (ES) provision by road verges, based on the literature review.

1. Field studies that include currently neglected ES (e.g. pollination and pest control), contexts (e.g. rural areas) and regions (e.g. Africa, Oceania and South America), and consider multiple ES, ecosystem disservices and potential trade-offs.
2. Field experiments of different road verge management scenarios and their effects on ES provision.
3. Analysis of how people derive ES from road verges, and of approaches to improve access to these ES.
4. Modelling of larger-scale ES provision (e.g. regional, national or international) by road verges under different management scenarios.
5. Modelling of road verge management scenarios, incorporating ES provision, ecosystem disservices and other environmental and social considerations alongside financial costs, to provide a holistic, long-term assessment.

8 | CONCLUSIONS

The potential of road verges for nature conservation is a rapidly growing area of interest in science (e.g. Gardiner et al., 2018) and society (e.g. Plantlife, 2019). We argue that this should go one step further by considering other ES and environmental benefits. Road verges have major potential to provide ES because they are widespread, located where people live and move, and are flexible in how they could be managed. Road verges are well placed to mitigate the negative ecological effects of roads and to address demand for ES in adjacent urban and agricultural landscapes. Road verges form a highly connected network that may facilitate the movement and dispersal of species and further enhance their provision of ES, but may also facilitate the dispersal of invasive species and increase vehicle–wildlife collisions. The global road network is projected to grow by 70% in length by 2050, which will cause many negative ecological and social impacts, but provides the opportunity to design and manage road verges explicitly to help mitigate these impacts. Road verge construction directly displaces habitats, so will largely have negative effects in natural landscapes, but might provide net gains in ES-impoverished urban and agricultural landscapes. The literature review highlighted large knowledge gaps, so we propose five priority areas for future research (Box 2).

Road verges should be valued for the ES that they currently provide to recognize them as an environmental asset. However, the capacity of road verges to provide ES might be enhanced considerably if they were strategically designed and managed for environmental outcomes, namely optimizing the selection, position and management of plant species and habitats. Low-cost opportunities to benefit biodiversity and ES include reducing mowing frequencies and planting trees in large verges. However, management of road verges for ES must also consider safety guidelines, financial costs, environmental costs of management, trade-offs between ES, and ecosystem disservices. Management can be costly, and current management of road verges often aims to reduce costs while meeting safety guidelines. In some cases, management for ES may be cheaper and provide a win–win, but in most other cases it will provide long-term financial returns if environmental benefits are accounted for, and could be incentivized through payment for ES (Richards & Thompson, 2019).

ACKNOWLEDGEMENTS

B.B.P. was funded by a NERC GW4+Doctoral Training Partnership studentship from the Natural Environment Research Council [NE/L002434/1], with additional funding from the Cornwall Area of Outstanding Natural Beauty unit. J.M.B. was funded under National Capability project NEO6895. The manuscript was improved by comments from two anonymous reviewers.

AUTHORS’ CONTRIBUTIONS

B.B.P. and K.J.G. conceived the ideas and led the writing of the manuscript. All authors contributed to the ideas, manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the University of Exeter’s Institutional Repository https://doi.org/10.871/39645 (Phillips, Bullock, Osborne, & Gaston, 2019).

ORCID

Benjamin B. Phillips https://orcid.org/0000-0003-4597-029X
James M. Bullock https://orcid.org/0000-0003-0529-4020
Kevin J. Gaston https://orcid.org/0000-0002-7235-7928

REFERENCES

Abhijith, K. V., Kumar, P., Gallagher, J., McNabola, A., Baldauf, R., Pilla, F., ... Pulvirenti, B. (2017). Air pollution abatement performances of green infrastructure in open road and built-up street canyon environments – A review. *Atmospheric Environment*, 162, 71–86. https://doi.org/10.1016/j.atmosenv.2017.05.014

Appelboom, T., Chescheir, G., Skaggs, R., & Hesterberg, D. (2002). Management practices for sediment reduction from forest roads in the coastal plains. *Transactions of the ASAE*, 45(2), 337–344. https://doi.org/10.13031/2013.8529

Baldauf, R. (2017). Roadside vegetation design characteristics that can improve local, near-road air quality. *Transportation Research Part D: Transport and Environment*, 52, 354–361. https://doi.org/10.1016/j.trd.2017.03.013

Bianchi, F. J. J. A., Goedhart, P. W., & Baveco, J. M. (2008). Enhanced pest control in cabbage crops near forest in the Netherlands. *Landscape Ecology*, 23(5), 595–602. https://doi.org/10.1007/s10980-008-9219-6

Black, J., Tara, K., & Pakzad, P. (2016). Mainstreaming green infrastructure elements into the design of public road reserves: Challenges for
International Energy Agency. (2013). Global land transport infrastructure requirements: Estimating road and railway infrastructure capacity and costs to 2050. Retrieved from https://www.iea.org/publications/publication/TransportInfrastructurefinal_FINAL_WEB.pdf

Jakobsson, S., Bernes, C., Bullock, J. M., Verheyen, K., & Lindborg, R. (2018). How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review. Environmental Evidence, 7, 1-14. https://doi.org/10.1186/s13750-018-0129-z

Jønáll, S. (2015). Review on urban vegetation and particle air pollution – Deposition and dispersion. Atmospheric Environment, 105, 130-137. https://doi.org/10.1016/j.atmosenv.2015.01.052

Kämpf, I., Hölzel, N., Störrle, M., Broll, G., & Kiehl, K. (2016). Potential of temperate agricultural soils for carbon sequestration: A meta-analysis of land-use effects. Science of the Total Environment, 566-567, 428-435. https://doi.org/10.1016/j.scitotenv.2016.05.067

Laurence, W. F., Clements, G. R., Sloan, S., O’Connell, C. S., Mueller, N. D., Funk, C. W., … Janhäll, S. (2015). Review on urban vegetation and particle air pollution – Deposition and dispersion. Environmental Management, 56, 2316-2327. https://doi.org/10.1111/1365-2664.13470

Lecumberri, M. A., & Verheyen, K. (2017). Ecosystem service delivery of green urban corridors: A comprehensive review. People and Nature, 5, 36. https://doi.org/10.1111/pan.12045

Lerer, M. C., Marcotte, S., Legras, M., Moncond’huy, V., Le Derf, F., & Portet-Koltalo, F. (2017). Influence of the vegetative cover on the habitat requirements of passerine birds. Landscape Ecology, 32, 2097-2103. https://doi.org/10.1007/s10980-015-0329-7

Lucey, A., & Barton, S. (2012). Public perception and sustainable management of transport infrastructure: A review. Transport Infrastructure Development, 21(2), 209-210. https://doi.org/10.1057/j.1365-2664.2015.03.006

Mitchell, M. G. E., Bennett, E. M., & Gonzalez, A. (2013). Linking landscape connectivity and ecosystem service provision: Current knowledge and research gaps. Ecosystems, 16, 894-908. https://doi.org/10.1007/s10021-013-9467-2

Mitchell, M. G. E., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., … Rhodes, J. R. (2015). Reframing landscape fragmentation effects on ecosystem services. Trends in Ecology and Evolution, 30(4), 190-198. https://doi.org/10.1016/j.tree.2015.01.011

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Werner, A., … Hayes, D. (2011). A large and persistent carbon sink the world’s forests. Science, 333, 988-993. https://doi.org/10.1126/science.1204588

Phillips, B. B., Bullock, J. M., Osborne, J. L., & Gaston, K. J. (2019). Data from: Ecosystem service provision by road verges. University of Exeter’s Institutional Repository, https://doi.org/10871/39645

Phillips, B. B., Gaston, K. J., Bullock, J. M., & Osborne, J. L. (2019). Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. Journal of Applied Ecology, 56, 2316-2327. https://doi.org/10.1111/1365-2664.13470

Piepensnieder, M., Bühle, L., Hensgen, F., & Wachendorf, M. (2016). Energy recovery from grass of urban roadside verges by anaerobic digestion and combustion after pre-processing. Biomass and Bioenergy, 85, 278-287. https://doi.org/10.1016/j.biombioe.2015.12.012

Plantlife. (2013). Flowers on the edge, press release. Retrieved from http://www.plantlife.org.uk

Plantlife. (2019). Road verge campaign. Retrieved from http://plantlife.net/love-wildflowers.org.uk/roadvergecampaign

Richards, D. R., & Thompson, B. S. (2019). Urban ecosystems: A new frontier for payments for ecosystem services. People and Nature, 1, 249-261. https://doi.org/10.1002/pan3.20

Salmon, J. A., Todaki, M., Vardoulakis, S., Arbuthnott, K., Coupts, A., Demuzere, M., … Wheeler, B. W. (2016). Health and climate related ecosystem services provided by street trees in the urban environment. Environmental Health, 15, 36. https://doi.org/10.1186/s12940-016-0103-6

Säumel, I., Weber, F., & Kowarik, I. (2016). Toward livable and healthy urban streets: Roadside vegetation provides ecosystem services where people live and move. Environmental Science and Policy, 62, 24-33. https://doi.org/10.1016/j.envsci.2015.11.012

Schwarz, N., Moretti, M., Bugalho, M. N., Davies, Z. G., Haase, D., Hack, J., … Knapp, S. (2017). Understanding biodiversity-ecosystem service relationships in urban areas: A comprehensive literature review. Ecosystem Services, 27, 161-171. https://doi.org/10.1016/j.ecoser.2017.08.014

Sodoudi, S., Zhang, H., Chi, X., Müller, F., & Li, H. (2018). The influence of spatial configuration of green areas on microclimate and thermal comfort. Urban Forestry and Urban Greening, 34, 85-96. https://doi.org/10.1016/j.ufug.2018.06.002

Stratopoulos, L. M. F., Duthweiler, S., Häberle, K. H., & Pauleit, S. (2018). Effect of native habitat on the cooling ability of six nursery-grown tree species and cultivars for future roadside plantings. Urban Forestry and Urban Greening, 30, 37-45. https://doi.org/10.1016/j.ufug.2018.01.011

Suárez-Esteban, A., Fahrig, L., Delibes, M., & Fedrani, J. M. (2016). Can anthropogenic linear gaps increase plant abundance and diversity? Landscape Ecology, 31, 721-729. https://doi.org/10.1007/s10980-015-0329-7

Townsend, P. A., & Levey, D. J. (2005). An experimental test of whether habitat corridors affect pollen transfer. Ecology, 86(2), 466-475. https://doi.org/10.1890/03-0607

Tremblay, M. A., & St. Clair, C. C. (2009). Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. Journal of Applied Ecology, 46(6), 1314-1322. https://doi.org/10.1111/j.1365-2664.2009.01717.x

United Nations. (2018). 2018 Revision of world urbanization prospects. Retrieved from https://population.un.org/wup/

United States Forest Service. (2019). i-Tree. Retrieved from http://www.itreetools.org/

Van Vooren, L., Reubens, B., Broeck, S., De Frenne, P., Nelissen, V., Pardón, P., & Verheyen, K. (2017). Ecosystem service delivery of agri-environment measures: A synthesis for hedgerows and grass strips on arable land. Agriculture, Ecosystems and Environment, 244, 32-51. https://doi.org/10.1016/j.agee.2017.04.015
Vasenev, V., & Kuzyakov, Y. (2018). Urban soils as hot spots of anthropogenic carbon accumulation: Review of stocks, mechanisms and driving factors. *Land Degradation and Development*, 29(6), 1607-1622. https://doi.org/10.1002/ldr.2944

Vilà, M., & P. Hulme (Eds.). (2017). *Impact of biological invasions on ecosystem services*. Berlin, Germany: Springer.

Villemey, A., Jeusset, A., Vargac, M., Bertheau, Y., Coulon, A., Touroult, J., ... Sordello, R. (2018). Can linear transportation infrastructure verges constitute a habitat and/or a corridor for insects in temperate landscapes? A systematic review. *Environmental Evidence*, 7(1), 1-33. https://doi.org/10.1186/s13750-018-0117-3

Voinov, A., Arodudu, O., Van Duren, I., Morales, J., & Qin, L. (2015). Estimating the potential of roadside vegetation for bioenergy production. *Journal of Cleaner Production*, 102, 213-225. https://doi.org/10.1016/j.jclepro.2015.04.034

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

---

**How to cite this article:** Phillips BB, Bullock JM, Osborne JL, Gaston KJ. Ecosystem service provision by road verges. *J Appl Ecol*. 2020;57:488-501. [https://doi.org/10.1111/1365-2664.13556](https://doi.org/10.1111/1365-2664.13556)