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REVIEW ARTICLE

Can anthropogenic linear gaps increase plant abundance and diversity?

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Abstract

Context Seed-dispersing animals often move along "linear gaps" (linear anthropogenic features such as roads and trails that contain little vegetation), especially in densely-vegetated landscapes. As a result, linear gaps and their verges may receive more seeds than adjacent habitats. In addition, linear gap verges may provide more suitable conditions for plant establishment than neighboring habitats. In this way, linear gaps may increase plant abundance and diversity, and facilitate connectivity of native and non-native plant populations, ultimately increasing plant diversity in the landscape.

Objectives We reviewed current evidence for the potential of anthropogenic linear gaps to increase plant abundance and diversity, and for the mechanisms involved.

Methods We reviewed peer-reviewed literature published up to December 31st, 2014.

Results Most (69.2 %) studies found significantly higher plant abundance and/or diversity in linear gap verges than in adjacent habitats. This suggests that linear gaps can increase plant abundance and diversity, and possibly facilitate population spread. However, there was a strong bias toward the study of exotic species. In addition, there were few mechanistic studies to allow estimation of the relative contributions of dispersal and post-dispersal mechanisms operating in linear gaps.

Conclusions Future studies should focus on entire plant communities, not just exotic species, and should

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allow identification of the mechanisms by which linear gaps increase plant abundance and diversity. With this knowledge in hand, we will be in a better position to understand whether the net benefit of linear gaps for plant diversity in general outweigh their facilitation of the spread of exotic species.

Keywords Corridor · Edge · Gene flow · Plant diversity · Plant invasion · Road · Seed dispersal

Introduction

Anthropogenic linear gaps in the landscape created for roads, railways, trails, power lines, seismic lines, and firebreaks, have become pervasive (Forman 1998), even within protected areas. For example, charismatic National Parks such as Yellowstone (USA; area = 8987 Km^2), Kruger (South Africa; 19,485 Km^2) and Doñana (Spain; 543 Km^2) each contain more than 2000 km of human-made linear gaps (data from respective websites). It is usually assumed that these linear gaps reduce biodiversity (Trombulak and Frissell 2000). For example, they represent the main driver of habitat fragmentation worldwide (Forman et al. 2003). They also greatly increase the amount of edge habitat in the landscape, which can have negative effects on some species and ecological processes (Laurance and Yensen 1991; Harper et al. 2005). However, linear gaps may also hold unforeseen conservation value.

Within highly vegetated landscapes, many animals move through linear gaps and defecate in their verges (Campbell and Gibson 2001; Mount and Pickering 2009; López-Bao and González-Varo 2011). These animals may carry seeds attached to their fur (Couvreur et al. 2004), or clothing (Mount and Pickering 2009; Taylor et al. 2012), or in their guts (Suárez-Esteban et al. 2013a). For example, terrestrial mammals such as red foxes (e.g. *Vulpes vulpes*; Rost et al. 2012), martens (*Martes* spp; López-Bao and González-lez-Varo 2011), weasels (e.g. *Mustela itatsi*; Tsuji et al. 2011) and lagomorphs (Suárez-Esteban et al. 2013a), as well as non-flying birds such as the cassowary (*Casuarius casuarius*; Stocker and Irvine 1983) are known to disperse seeds along the linear gap verges. In addition, some birds such as the Eurasian jay (*Garrulus glandarius*) may hoard seeds in linear gap verges (Pons and Pausas 2007). Seed dispersal

along linear gap verges has also been documented in domestic animals such as horses, dogs and cattle (Kiviniemi and Eriksson 1999; Campbell and Gibson 2001; Graae 2002; Stroh and Struckhoff 2009). Seeds dispersed by wind or water may also accumulate along linear gap verges (Soomers et al. 2013).

Given the widespread use of linear gaps by seed dispersers, linear gap verges may receive a disproportionate number of seeds (Suárez-Esteban et al. 2013a). Linear gap verges may also provide a more suitable light environment for plant establishment than surrounding habitats (Parendes and Jones 2000; Arévalo et al. 2005). Furthermore, water and nutrients may be more abundant along linear gap verges such as ditches and roadsides than in adjacent habitats (Harper and Macdonald 2002; Christen and Matlack 2006; Neher et al. 2013). Finally, linear gaps are generally maintained as gaps by management actions. On linear gap verges, however, management actions may increase plant diversity by emulating natural disturbance regimes (Spooner et al. 2004; Irl et al. 2014).

If linear gap verges receive more seeds and the seeds that land are more likely to germinate there than in neighboring habitats, this may translate into higher plant abundance and diversity along linear gap verges than in adjacent habitats. This would have implications for landscape connectivity, biological invasions, and biodiversity conservation. However, the possibility that linear gaps increase plant abundance and diversity has been largely overlooked and not systematically reviewed.

Here, we review evidence for the prediction that anthropogenic linear gaps increase plant abundance and diversity. Specifically, we ask three questions: (1) Are plant abundance and diversity higher in linear gap verges than in adjacent habitats? (2) If so, what are the underlying mechanisms for this? Finally, (3) do linear gaps promote plant population spread? Our goal is to stimulate new research and discussion among landscape ecologists, conservation biologists, and landscape managers on the ecological roles of anthropogenic linear gaps.

Methods

Literature review

Using the browser Scopus, we reviewed published peer-reviewed studies on plant abundance and

diversity along linear gaps, using all potential combinations of the terms "plant abundance", "plant diversity", "plant spread", "plant expansion", "plant colonization", "plant dispersal", "seed dispersal", "seed arrival", "seed deposition", "seed rain" and "seed shadow", and the terms "gap", "road", "linear feature", "clearing", "clearcut", "opening", "power line", "railway", "trail", "seismic line", "ditch" and "channel", as well as some studies cited in the papers we found. We limited our search to studies published up to December 31st, 2014. We found 295 papers that matched our search terms. In the end we reviewed 218 studies that were relevant to our questions.

Quantitative analyses

We extracted plant abundance and diversity estimates from 49 studies and calculated their ratios in linear gaps and adjacent habitats. We used the ratio to standardize for differences between studies in overall abundance and diversity metrics.

As studies comparing plant abundance/diversity in linear gaps and adjacent habitats had a common null hypothesis (no difference), we conducted a simple meta-analysis using the Fisher's combined probability test (Chen 2011). This test requires p-values, which we obtained for 47 studies. We could not perform a more refined meta-analysis because the number of studies was limited, authors generally did not report effect sizes, and different studies reported different plant abundance and diversity measures, making standardization challenging. We could not conduct Fischer tests for our questions 2 and 3 because of the lack of studies addressing these issues.

Results and discussion

Are plant abundance and diversity higher in linear gap verges than in adjacent habitats?

We found 133 studies that measured plant abundance and/or diversity in linear gap verges, but only 65 compared these values to abundance/diversity in adjacent habitats. Of these, 45 (69.2 %) found higher plant abundance and/or diversity in linear gap verges than in adjacent habitats (Table A1; Fig. 1). For example, Hovd and Skogen (2005), Zeng et al. (2011) and Azcárate et al. (2013) found ratios of 1.34, 1.38

and 4.9 times higher mean species richness in road verges than in adjacent human-modified habitats (e.g. agricultural lands, oil fields), respectively. Similarly, O'Farrell and Milton (2006) and Suárez-Esteban et al. (2013b) found ratios of 1.45 and 1.32 for plant abundances in roadsides versus adjacent scrublands. Higher plant abundance and diversity in linear gap verges as compared with adjacent habitats was also reported in other ecosystems and linear gap types (Table A1).

Only 10 (15.4 %) studies found lower plant abundance and/or diversity in linear gap verges than in adjacent habitats (Table A1). Specifically, Gorchov et al. (1993), Kemper and MacDonald (2009), and Lee et al. (2012) found that mean plant species richness in linear clearings, seismic lines and road verges was 0.19, 0.74, and 0.68 times lower than those of adjacent tropical rainforests, tundra, and grasslands, respectively. Interestingly, Vasconcelos et al. (2014) found that, despite overall plant species richness being higher in road verges than in the adjacent Cerrado forest, the abundance of most species was higher in forest interior than in linear gap verges. Finally, seven (10.8 %) studies did not find significant differences between linear gap verges and adjacent habitats (Table A1).

We found consistent evidence across our reviewed studies for the hypothesis that linear gaps can increase both plant abundance (Fisher's combined probability test; n = 23, $\chi^2 = 273.47$, df = 46, $P < 0.0001$) and diversity (n = 24, $\chi^2 = 239.56$, df = 48, $P < 0.0001$; Fig. 1).

What are the mechanisms that determine plant abundance and diversity in linear gaps?

Plant abundance and diversity depend on both dispersal (i.e. seed arrival) and post-dispersal processes (seed survival and germination, seedling survival, sapling growth; Rey and Alcántara 2000; Gómez-Aparicio 2008; Schupp et al. 2010). Both dispersal and post-dispersal processes may be affected by linear gaps.

Seed abundance in linear gaps versus adjacent habitats

We found 38 studies that measured seed abundance in linear gap verges. Only eight studies of these
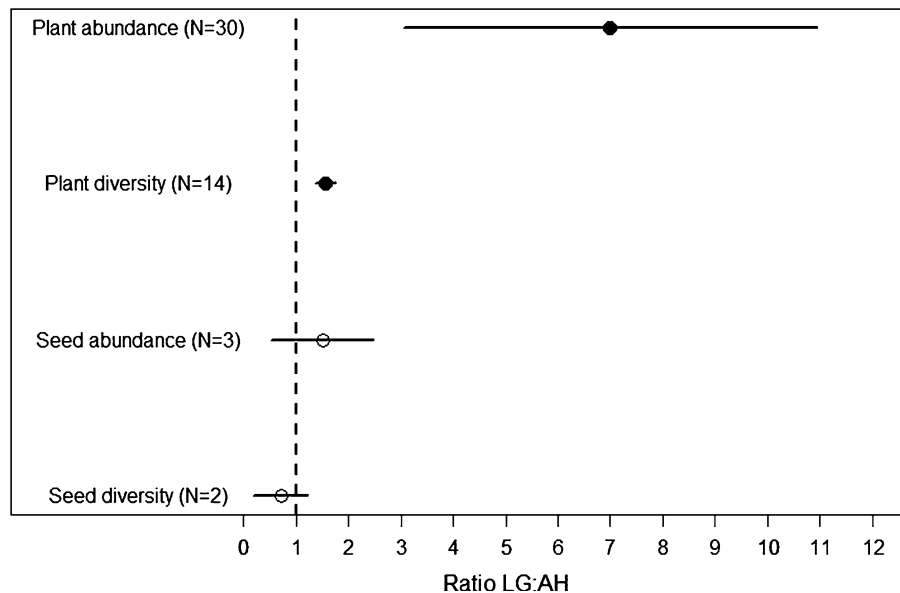
compared seed abundance in linear gap verges and adjacent habitats. Of these, four studies found higher seed abundance in linear gap verges than in adjacent habitats (Table A1). This difference is not necessarily due to differences in dispersal. This could be due to three non-exclusive mechanisms. First, more seeds may be produced in linear gap verges than in adjacent habitats. For example, Honu and Gibson (2008) found that seed abundance of 26 plant species inhabiting roadsides declined from linear gaps into the interior of oak forests. This may be due to higher plant densities and/or to a higher seed set per plant. Meekins and McCarthy (2001) found that the per-plant reproductive rate of *Alliaria petiolata* in forest road verges was 2.5 times greater on average than in forest interiors.

A second mechanism that may explain higher seed abundance in linear gap verges than in adjacent habitats is higher seed deposition by animal dispersers in linear gap verges than in adjacent habitats. Such difference has been shown for plants dispersed by birds (Pons and Pausas 2007), other wildlife (Suárez-Esteban et al. 2013a), and humans (Veldman and Putz 2010).

The third possible explanation is that seed banks may be more persistent in linear gaps than in adjacent habitats. For example, Burkey (1993) found lower seed predation rates in linear gap verges than in adjacent habitats. On the other hand, Suárez-Esteban (2013) found that post-dispersal seed predation was

overall similar between trail/firebreak verges and adjacent scrublands.

Of the eight studies comparing seed abundance in linear gap verges and adjacent habitats, three found fewer seeds in gap verges, and one found no significant differences (Table A1).

To summarize, we found strong support for the prediction that plant abundance and diversity are higher in linear gap verges than in neighboring habitats, but we did not find support for the idea that this difference is due to higher seed abundance in linear gap verges (Fig. 1). This could be due to the small number of studies (8) that compared seed abundance in linear gaps and adjacent habitats. In addition, the influence of linear gaps on seed abundance may differ depending on the linear gap type, an area that remains underexplored.

The lack of consistent support for the prediction that seed abundance should be higher in linear gap verges than adjacent habitats may also be explained by differences in adjacent habitat type. If the surrounding habitats are vegetated but open, then we would not expect gaps to represent dispersal paths, and so seed deposition would not occur disproportionately in linear gaps. In three of the four studies that found higher seed abundance in linear gap verges than in adjacent habitats, adjacent habitats were forests or dense scrublands.

A final possible explanation for the lack of consistent results is that the influence of linear gaps on seed dispersal is species-dependent, with some species being preferentially dispersed to linear gap verges and others showing the opposite or no pattern (Suárez-Esteban et al. 2013a). This suggests that to determine whether seed abundance is generally higher in linear gap verges than in adjacent habitats entire plant communities should be studied rather than single species.

Post-dispersal mechanisms in linear gaps versus adjacent habitats

Even if linear gaps do not receive more seeds than adjacent habitats, they could still promote plant population increase if plant establishment and growth rates are higher in linear gaps than in adjacent habitats. Although several studies have highlighted the high habitat quality of some linear gap verges, due to, for example, high amounts of light/nutrients, or low competition/predation (Parendes and Jones 2000; Campbell and Gibson 2001; Maheu-Giroux and De Blois 2007; Stroh and Struckhoff 2009; Brisson et al. 2010; Cipriotti et al. 2010; Veldman and Putz 2010), we found only four studies that compared post-dispersal processes in linear gaps versus adjacent habitats.

Meekins and McCarthy (2001), Aragón and Groom (2003), and Christen and Matlack (2009) found higher germination rates in gaps and edges than in adjacent habitats, while Suárez-Esteban (2013) found no consistent differences in seed or seedling survival and establishment between linear gaps and adjacent habitats.

Finally, the relative contributions of dispersal and post-dispersal mechanisms to plant abundance and diversity in linear gaps may change over time. For example, if linear gaps are not periodically maintained, the amount of light reaching linear gap verges may decrease as succession progresses (Harper and Macdonald 2002; Harper et al. 2005). This may in turn change the relative contribution of dispersal and post-dispersal mechanisms in linear gaps. For example, if light becomes limiting, the arrival of more seeds to linear gaps may not necessarily translate into higher plant abundance in linear gaps than in adjacent habitats. This temporal component should be considered in systematic examinations of the effects of linear gaps on plant communities (Fig. 2).

Do linear gaps promote plant population spread?

We can only conclude that a linear gap assists plant spread if, from a given starting point, a population extends more quickly along the linear gap than in adjacent habitats. Lelong et al. (2007) and Blanchet et al. (2014) used genetic methods to reconstruct the spread history of *Phragmites australis* in Quebec, Canada, and *Senecio inaequidens* in France. They concluded that roads and railways have probably assisted the spread of these invasive species into previously unoccupied areas. However, we did not find any studies that systematically compared plant spread rates between linear gaps and adjacent habitats.

The influence of linear gaps on plant communities, with conservation implications

Thirty-two out of the 45 studies that found higher plant abundance and/or diversity in linear gap verges than in adjacent habitats focused on exotic species (Table A1). Higher abundance and diversity of exotic plant species along linear gap verges may facilitate the spread of these species into adjacent habitats through a spillover effect (Brudvig et al. 2009), which could have negative effects on native plant communities. In this case, linear gaps could be viewed as undesirable corridors (Proches et al. 2005).

On the other hand, linear gaps are relatively narrow areas where it might be possible to effectively focus efforts to stop the spread of unwanted exotic species. For exotic species with low spread rates, it might be more effective to perform intense but infrequent eradication campaigns, while for species with high spread rates, it might be more effective to perform less intense but frequent eradication campaigns (Christen and Matlack 2006). Seed dispersal models (Westcott et al. 2008) and remote sensing (Bradley and Mustard 2006) can help managers decide when and where to focus eradication resources.

Linear gaps also have the potential to assist the conservation of native plant species, even rare or endangered (Baltzinger et al. 2011; Catling and Kostiuk 2011; Suárez-Esteban et al. 2013b). For example, linear gaps may host incipient plant populations acting as stepping stones that provide a seed
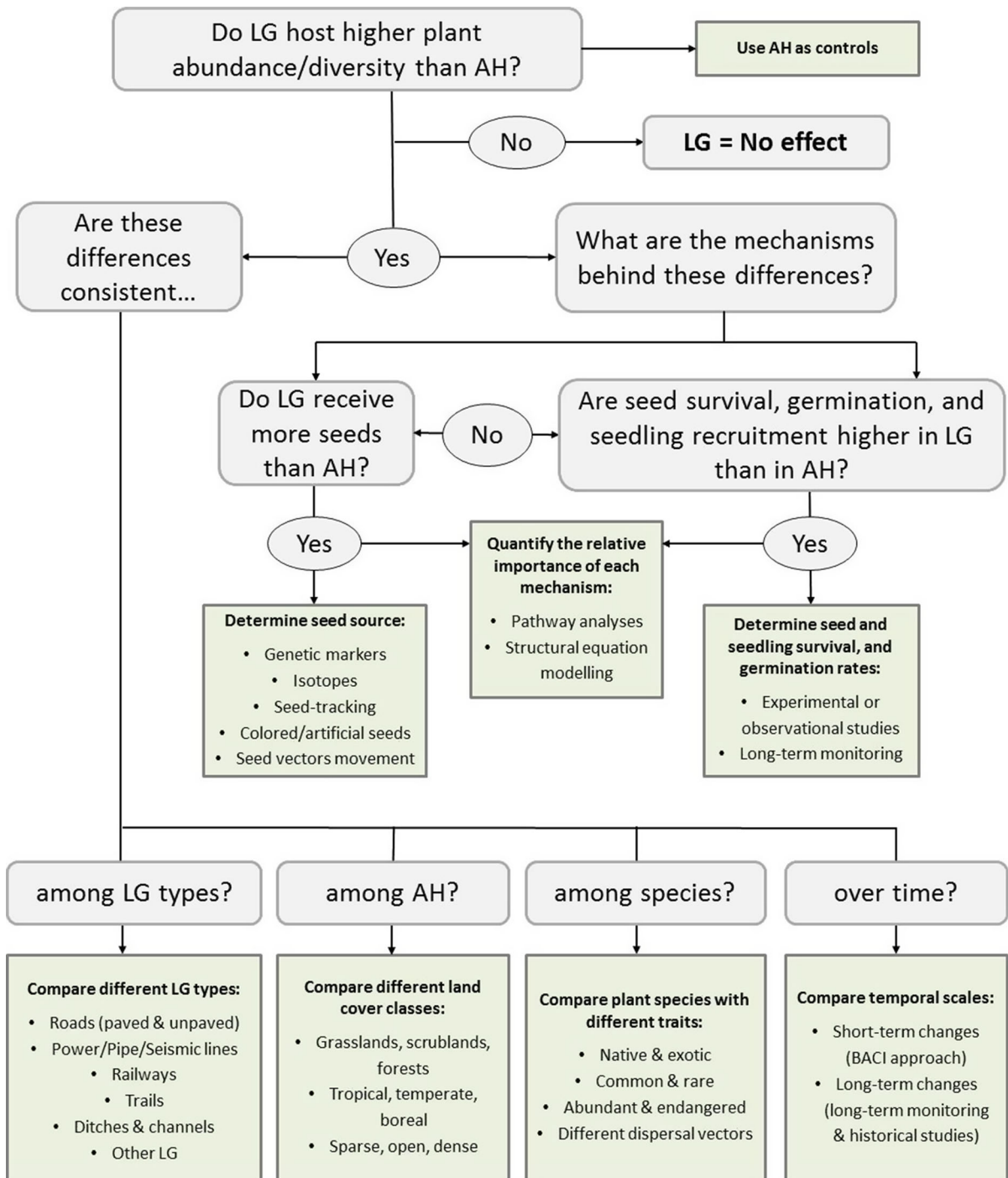
Fig. 2 Diagram showing suggested research lines to improve our understanding of the effects of linear gaps (LG) on plant abundance and diversity, and of the mechanisms behind them. Note that adjacent habitats (AH) must always be included as a control. BACI (Before–After–Control–Impact) studies would quantify plant abundance and diversity both before and after the creation of a linear gap at both gap sites and non-gap sites

source at an intermediate distance between primary habitat areas (Suárez-Esteban et al. 2013b). As such, linear gaps may provide plant migration routes in response to climate change (Williams et al. 2005), increase connectivity between otherwise isolated populations, and promote plant species richness at large scales (Damschen et al. 2006). This potential role is especially relevant in human-dominated landscapes, where linear gaps could act as refugia for some species (Hovd and Skogen 2005; Zeng et al. 2011; Azcárate et al. 2013; Zielińska et al. 2013). These potential positive effects of linear corridors suggest that it will be important to know, in a given situation, whether a linear gap functions as a corridor both for exotic and native species, so that eradication methods are chosen that target the former and not the latter.

Synthesis, caveats, and future research

Our review suggests that anthropogenic linear gaps can increase plant abundance and diversity. However, the results may be biased. Researchers may tend to study the effects of linear gaps only on plants species for which they noticed a difference. This is likely the reason for the prevalence of studies on exotic species. A more accurate conclusion may therefore be that linear gaps increase the abundance and diversity of exotic plant species. Before concluding that this result applies to plants in general, we need more studies comparing the abundance and diversity of both native and exotic plant species between randomly chosen linear gaps and their adjacent habitats.

Even if studies confirmed that linear gaps increase plant abundance and diversity, very little is known about the context dependency of these effects. For example, measures of plant abundance and diversity may differ from linear gap verges to the center (Gorchov et al. 1993; Greene and Johnson 1996), among different types of linear gaps, and also over time in the same linear gap. A comprehensive understanding of the effects of linear gaps on plants would require comparing abundance and diversity of entire plant communities between different linear gap types and different surrounding habitats, consistently measured in the same relative position within the gap, and over time (Fig. 2).

The mechanisms generating differences in plant abundance and diversity between linear gaps and adjacent habitats are barely understood. The hypothesis that linear gaps receive more seeds, either locally produced or through dispersal, than adjacent habitats remains underexplored. This can be rectified by studies that survey seed abundance along transects or in plots placed both in linear gaps and in adjacent habitats (Veldman and Putz 2010; Suárez-Esteban et al. 2013a). Documenting where the seeds came from would require using more sophisticated methods such us genetic markers (González-Varo et al. 2014), isotopes (Carlo et al. 2012), radio-tracking (Pons and Pausas 2007), artificial seeds (Damschen et al. 2014), colored seeds (Lemke et al. 2009), or a thorough knowledge of how the movement of dispersal vectors is influenced by landscape structure (Brodie et al. 2009). In addition to seed deposition, it is important to understand how linear gaps influence post-dispersal processes (Blomqvist et al. 2003). Full life-cycle analyses are therefore needed to fully understand the role of linear gaps in the persistence of a given species (Fig. 2). On the other hand, this type of analysis cannot be done for every species in a plant community. An overall picture of the role of linear gaps on plants therefore will depend on an unbiased selection of species for in-depth study and analysis.

Given that anthropogenic linear gaps are pervasive, their potential influence on plant abundance, diversity and spread represents a relatively unexplored frontier in ecological knowledge, and a challenging opportunity for biodiversity conservation and restoration ecology. More comprehensive and unbiased empirical investigation should be a priority.

References

Aragón R, Groom M (2003) Invasion by *Ligustrum lucidum* (*Oleaceae*) in NW Argentina: early stage characteristics in different habitat types. Rev Biol Trop 51(1):59–70

Arévalo JR, Delgado JD, Otto R, Naranjo A, Salas M, Fernández-Palacios JM (2005) Distribution of alien versus native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect Plant Ecol Evol Syst 7(3):185–202

Azcárate FM, Robleño I, Seoane J, Manzano P, Peco B (2013) Drove roads as local biodiversity reservoirs: effects on landscape pattern and plant communities in a Mediterranean region. Appl Veg Sci 16(3):480–490

Baltzinger M, Archaux F, Gosselin M, Chevalier R (2011) Contribution of forest management artefacts to plant diversity at a forest scale. Ann For Sci 68(2):395–406

Blanchet É, Penone C, Maurel N, Billot C, Rivallan R, Risterucci AM, Maurice S, Justy F, Machon N, Noël F (2014) Multivariate analysis of polyploid data reveals the role of railways in the spread of the invasive South African Ragwort (*Senecio inaequidens*). Conserv Genet 16(3):523–533

Blomqvist MM, Vos P, Klinkhamer PGL, Ter Keurs WJ (2003) Declining plant species richness of grassland ditch banks: a problem of colonisation or extinction? Biol Conserv 109(3):391–406

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. Ecol Appl 16(3):1132–1147

Brisson J, De Blois S, Lavoie C (2010) Roadside as invasion pathway for common reed (*Phragmites australis*). Invasive Plant Sci Manag 3(4):506–514

Brodie JF, Helmy OE, Brockelman WY, Maron JL (2009) Functional differences within a guild of tropical mammalian frugivores. Ecology 90(3):688–698

Brudvig LA, Damschen EI, Tewksbury JJ, Haddad NM, Levey DJ (2009) Landscape connectivity promotes plant biodiversity spillover into non-target habitats. Proc Natl Acad Sci USA 106(23):9328–9332

Burkey TV (1993) Edge effects in seed and egg predation at two neotropical rainforest sites. Biol Conserv 66(2):139–143

Campbell JE, Gibson DJ (2001) The effect of seeds of exotic species transported via horse dung on Vegetation along trail corridors. Plant Ecol 157(1):23–35

Carlo TA, García D, Martínez D, Gleditsch JM, Morales JM (2012) Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. Ecology 94(2):301–307

Catling PM, Kostiuk B (2011) Some wild canadian orchids benefit from woodland hiking trails—and the implications. Can Field Nat 125(2):105–115

Chen Z (2011) Is the weighted z-test the best method for combining probabilities from independent tests? J Evol Biol 24(4):926–930

Christen DC, Matlack GR (2006) The role of roadsides in plant invasions: a demographic approach. Conserv Biol 20(2):385–391

Christen DC, Matlack GR (2009) The habitat and conduit functions of roads in the spread of three invasive plant species. Biol Invasions 11(2):453–465

Cipriotti PA, Rauber RB, Collantes MB, Braun K, Escartín C (2010) *Hieracium pilosella* invasion in the Tierra del Fuego steppe, Southern Patagonia. Biol Invasions 12(8):2523–2535

Couvreur M, Christiaen B, Verheyen K, Hermy M (2004) Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. Appl Veg Sci 7(2):229–236

Damschen EI, Baker DV, Bohrer G, Nathan R, Orrock JL, Turner JR, Brudvig LA, Haddad NM, Levey DJ, Tewksbury JJ (2014) How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. Proc Natl Acad Sci 111(9):3484–3489

Damschen EI, Haddad NM, Orrock JL, Tewksbury JJ, Levey DJ (2006) Corridors increase plant species richness at large scales. Science 313(5791):1284–1286

Forman RTT (1998) Road ecology: a solution for the giant embracing us. Landscape Ecol 13(4):iii–v

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) Road ecology: science and solutions. Island Press, Washington

Gómez-Aparicio L (2008) Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. J Ecol 96(6):1128–1140

González-Varo JP, Arroyo JM, Jordano P (2014) Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. Methods Ecol Evol 5(8):806–814

Gorchov DL, Cornejo F, Ascorra C, Jaramillo M (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107–108(1):339–349

Graae BJ (2002) The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. Seed Sci Res 12(2):113–121

Greene DF, Johnson EA (1996) Wind dispersal of seeds from a forest into a clearing. Ecology 77(2):595–609

Harper KA, Macdonald SE (2002) Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. J Veg Sci 13(4):535–546

Harper KA, Macdonald SE, Burton PJ, Chen J, Brosofske KD, Saunders SC, Euskirchen ES, Roberts DA, Jaiteh MS, Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19(3):768–782

Honu YAK, Gibson DJ (2008) Patterns of invasion: trends in abundance of understory vegetation, seed rain, and seed bank from forest edge to interior. Nat Areas J 28(3):228–239

Hovd H, Skogen A (2005) Plant species in arable field margins and road verges of central Norway. Agric Ecosyst Environ 110(3–4):257–265

Irl SDH, Steinbauer MJ, Epperlein L, Harter DE, Jentsch A, Pätz S, Wohlfart C, Beierkuhnlein C (2014) The Hitchhiker's guide to island endemism: biodiversity and endemic perennial plant species in roadside and surrounding vegetation. Biodivers Conserv 23(9):2273–2287

Kemper J, MacDonald S (2009) Effects of contemporary winter seismic exploration on low arctic plant communities and permafrost. Arct Antarct Alp Res 41(2):228–237

Kiviniemi K, Eriksson O (1999) Dispersal, recruitment and site occupancy of grassland plants in fragmented habitats. Oikos 86(2):241–253

Laurance WF, Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. Biol Conserv 55(1):77–92

Lee MA, Davies L, Power SA (2012) Effects of roads on adjacent plant community composition and ecosystem function: an example from three calcareous ecosystems. Environ Pollut 163:273–280

Lelong B, Lavoie C, Jodoin Y, Belzile F (2007) Expansion pathways of the exotic common reed (*Phragmites australis*): a historical and genetic analysis. Divers Distrib 13(4):430–437

Lemke A, Von Der Lippe M, Kowarik I (2009) New opportunities for an old method: using fluorescent colours to measure seed dispersal. J Appl Ecol 46(5):1122–1128

López-Bao JV, González-Varo JP (2011) Frugivory and spatial patterns of seed deposition by carnivorous mammals in anthropogenic landscapes: a multi-scale approach. PLoS One 6(1):e14569

Maheu-Giroux M, De Blois S (2007) Landscape ecology of *Phragmites australis* invasion in networks of linear wetlands. Landscape Ecol 22(2):285–301

Meekins JF, McCarthy BC (2001) Effect of environmental variation on the invasive success of a nonindigenous forest herb. Ecol Appl 11(5):1336–1348

Mount A, Pickering CM (2009) Testing the capacity of clothing to act as a vector for non-native seed in protected areas. J Environ Manag 91(1):168–179

Neher DA, Asmussen D, Lovell ST (2013) Roads in northern hardwood forests affect adjacent plant communities and soil chemistry in proportion to the maintained roadside area. Sci Total Environ 449:320–327

O'Farrell PJ, Milton SJ (2006) Road verge and rangeland plant communities in the southern Karoo: exploring what influences diversity, dominance and cover. Biodivers Conserv 15(3):921–938

Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Conserv Biol 14(1):64–75

Pons J, Pausas JG (2007) Acorn dispersal estimated by radio-tracking. Oecologia 153(4):903–911

Proches S, Wilson JRU, Veldtman R, Kalwij JM, Richardson DM, Chown SL (2005) Landscape corridors: possible dangers? Science 310(5749):779–783

Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. J Ecol 88(4):622–633

Rost J, Pons P, Bas JM (2012) Seed dispersal by carnivorous mammals into burnt forests: an opportunity for non-indigenous and cultivated plant species. Basic Appl Ecol 13(7):623–630

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytol 188(2):333–353

Soomers H, Karssenberg D, Soons MB, Verweij PA, Verhoeven JTA, Wassen MJ (2013) Wind and water dispersal of wetland plants across fragmented landscapes. Ecosystems 16(3):434–451

Spooner PG, Lunt ID, Briggs SV, Freudenberger D (2004) Effects of soil disturbance from roadworks on roadside shrubs in a fragmented agricultural landscape. Biol Conserv 117(4):393–406

Stocker GC, Irvine AK (1983) Seed dispersal by Cassowaries (*Casuarius casuarius*) in north Queensland's rainforests. Biotropica 15(3):170–176

Stroh ED, Struckhoff MA (2009) Exotic plant species associations with horse trails, old roads, and intact native communities in the Missouri Ozarks. Nat Areas J 29(1):50–56

Suárez-Esteban A (2013) Ecological engineers in Doñana: combined effect of linear structures and plant-animal interactions on the Mediterranean scrubland. University of Oviedo, Oviedo

Suárez-Esteban A, Delibes M, Fedriani JM (2013a) Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal. J Appl Ecol 50(3):767–774

Suárez-Esteban A, Delibes M, Fedriani JM (2013b) Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment. Biol Conserv 167:50–56

Taylor K, Brummer T, Taper ML, Wing A, Rew LJ (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Divers Distrib 18(9):942–951

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14(1):18–30

Tsuji Y, Tatewaki T, Kanda E (2011) Endozoochorous seed dispersal by sympatric mustelids, *Martes melampus* and *Mustela itatsi*, in western Tokyo, central Japan. Mamm Biol 76(5):628–633

Vasconcelos PB, Araújo GM, Bruna EM (2014) The role of roadsides in conserving Cerrado plant diversity. Biodivers Conserv 23(12):3035–3050

Veldman JW, Putz FE (2010) Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica 42(6):697–703

Westcott DA, Setter M, Bradford MG, McKeown A, Setter S (2008) Cassowary dispersal of the invasive pond apple in a tropical rainforest: the contribution of subordinate dispersal modes in invasion. Divers Distrib 14(2):432–439

Williams P, Hannah LEE, Andelman S, Midgley GU, AraúJo M, Hughes G, Manne L, Martinez-Meyer EN, Pearson R (2005) Planning for climate change: identifying minimum-dispersal corridors for the cape Proteaceae. Conserv Biol 19(4):1063–1074

Zeng SL, Zhang TT, Gao Y, Ouyang ZT, Chen JK, Li B, Zhao B (2011) Effects of road age and distance on plant biodiversity: a case study in the Yellow River Delta of China. Plant Ecol 212(7):1213–1229

Zielińska KM, Misztal M, Zielińska A, Zywiec AM (2013) Influence of ditches on plant species diversity in the managed forests of Central Poland. Balt For 19(2):270–279