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Effects of past pollution on zoochory in a recovering mixed temperate–boreal forest[1]

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Abstract: In landscapes perturbed by industrial mining, seed dispersal limitations could affect the potential for forest recovery. We measured seed removal in different vegetation layers by different dispersal vectors to examine the potential for natural recovery of a severely stressed forest in Greater Sudbury, Canada. Vegetation structure was measured and causal relationships with seed removal along a stress gradient of past pollution were estimated using path analysis. There was almost no seed removal in the most degraded sites, and birds removed fewer seeds than other animal groups in all sites. An increasing trend across the pollution gradient was identified for both seed types examined (blueberries and oaks), and it was strongly correlated with basal area per hectare, distance to decommissioned smelter, and understory cover. A negative effect of an invasive slug species on the seed consumption process was detected. We show slow recovery in more degraded sites, the importance of forest structure for animal activity, and the need for considering structural and functional components when analyzing regeneration from past pollution.
Keywords: copper–nickel smelter, plant–animal interaction, *Quercus rubra*, seed dispersal/predation, *Vaccinium angustifolium*.

Résumé : Dans des paysages perturbés par l'exploitation minière, certaines limites à la dispersion des graines pourraient avoir un effet sur le potentiel de rétablissement de la forêt. Nous avons mesuré le prélèvement de graines par divers vecteurs de dispersion dans différentes couches de végétation pour examiner le potentiel de rétablissement naturel d'une forêt soumise à un stress sévère dans la grande région de Sudbury au Canada. Nous avons évalué la structure végétale et estimé les relations causales avec le prélèvement de graines le long d'un gradient de stress dû à une pollution passée en utilisant une analyse de coefficients de direction. Il n'y avait presque aucun prélèvement de graines dans les sites les plus dégradés, et dans tous les sites, les oiseaux ont prélevé moins de graines que les autres groupes d'animaux. Une tendance vers une augmentation du prélèvement a été observée le long du gradient de diminution de la pollution pour les deux types de graines examinés (bleuets et chênes). Le prélèvement était fortement corrélé avec la surface terrière par hectare, la distance à la fonderie déclassée et la couverture végétale en sous-étage. Un effet négatif d'une espèce envahissante de limace sur la consommation de graines a été détecté. Nous montrons que le rétablissement est lent dans les sites plus dégradés, que la structure forestière est importante pour l'activité animale et qu'il est nécessaire de prendre en considération les composantes structurelles et fonctionnelles lors de l'analyse de la régénération forestière à la suite d'une pollution passée.
Mots-clés : dispersion/prédation de graines, fonderie de cuivre-nickel, interaction plantes-animaux, *Quercus rubra*, *Vaccinium angustifolium*.

Nomenclature: International Commission on Zoological Nomenclature, online; Newmaster & Ragupathy, online.

Introduction

Human activities have transformed a large proportion of the world's land surface, causing rapid biodiversity decline and raising concern about the potential negative effects on ecosystem functioning and the services that they provide (Chapin *et al.*, 2000). Under an increasing human demand for resources, challenges arise regarding the resilience and recovery potential of ecosystem functioning (Bennett & Balvanera, 2007). Since the beginning of the 20th century, air pollution has been (and continues to be) one of the major habitat stressors and sources of degradation worldwide. Due to the unique characteristics of point source emissions of smelters in the landscapes, this stressor presents an opportunity to analyze the effects along a gradient of intensity (Kozlov & Zvereva, 2011). Typically, there is an industrial barren area surrounding the source generated largely by clearcutting and fire and characterized by sparse vegetation and denuded land, leading to thin soil layers due to water and wind erosion. Further away from the point source the stress level decreases, but a decline of vegetation cover and diversity due to toxicity from the source of pollution can still be found (Anand & Desrochers, 2004; Anand, Laurence & Rayfield, 2005; Kozlov & Zvereva, 2007; Zvereva, Toivonen & Kozlov, 2008).

Habitat fragmentation and loss can also affect the abundance and distribution of fauna. For example, some birds and mammals avoid open areas due to higher predation risk,

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while others may be attracted by the presence of food in these areas (García & Chacoff, 2007). In particular, when forests have been exposed to long-term pollutant emissions a decrease in species richness and diversity of several taxa has been detected, as seen in arthropods (Perner *et al.*, 2003; Babin-Fenske & Anand, 2011) and mammals (Kataev, Suornela & Palokangas, 1994; Robitaille & Linley, 2006). Using a meta-analysis, Kozlov and Zvereva (2011) found that most trophic groups were negatively affected in diversity and abundance, except for primary consumers.

In forest ecosystems, when human activities deplete resources needed for natural regeneration (*e.g.*, deforestation, soil degradation), the recovery potential is limited by the availability of seeds to disperse and establish in a particular area. Thus, the recovery may depend on the arrival of wind- and animal-dispersed seeds (García, Zamora & Amico, 2010). Seed dispersal and predation by fauna have a direct influence on regeneration processes and successional patterns of many ecosystems, affecting species distribution and community structure. While seed predation is a common fate of seeds consumed by animals (Willson & Traveset, 2000; Farwig *et al.*, 2008), secondary seed dispersal (significant movement of viable seeds by insects, birds, and mammals, following initial dispersal) is an important process in the reproductive cycle of many species, facilitating long distance dispersal (Wunderle, 1997; Herrera & García, 2010). Because of its role in the potential movement of seeds from mature habitats into degraded patches, zoochory is important for plant persistence in fragmented landscapes (Herrera & García, 2010).

The role of dispersal limitation may also vary depending on the type of dispersal syndrome of the plant species. In temperate forest, more than 80% of tree species are anemochorous, while tropical forests show between 10 and 30% anemochory (Willson & Traveset, 2000; Leithead *et al.*, 2012). Nevertheless, animal dispersal limitation due to fragmentation and forest degradation may also have a strong effect in temperate forests, where 60% of shrub and herb species can possess zoochory as a dispersal syndrome (Forget *et al.*, 2011; Leithead *et al.*, 2012). Thus, in temperate forests, the different vegetation layers may respond differently, depending on the dominant dispersal syndrome. Although this all may in turn affect forest regeneration, the relationship between habitat modification and potential natural regeneration due to animal dispersion has been poorly explored in temperate forests.

In this study, we focus on the seed consumption process to examine the potential for natural recovery of the damaged temperate forest ecosystems surrounding the city of Greater Sudbury (Ontario, Canada). In this region the point source emissions were mainly of SO_2 and heavy metal particulates, resulting in decreasing vegetation loss and damage with increasing distance from the point source. Since 1972, older smelters have been decommissioned and closed, and new smelter emissions have been reduced by almost 90% (Gunn *et al.*, 1995). Nevertheless, these industrial stressors may have influenced the ability of the landscape to naturally restore itself (Kozlov & Zvereva, 2007). For example, soils close to the point source still have high heavy metal concentration, negatively affecting biomass (Anand *et al.*, 2003). Thus, our objectives were to 1) quantify and compare patterns of seed removal by different vertebrates as a proxy for seed dispersal/predation across the gradient for plants of different layers; 2) quantify and compare vegetation structure and composition along a pollution gradient; and 3) assess the relationship between vegetation structure and seed removal.

Methods

STUDY SITE

Vegetation samples were collected and seed removal experiments were conducted in naturally recovering sites within Greater Sudbury, Ontario, Canada (46° 30' N, 81° 00' W) (Figure 1). This region is characterized by the Great Lakes–St. Lawrence forest, a transition forest between the Carolinian deciduous forest and the Boreal coniferous forest, characterized by red pine (*Pinus resinosa*), white birch (*Betula papyrifera*), and white pine (*Pinus strobus*), and features shallow soils due to the occurrence of Canadian Shield bedrocks. Temperatures range from 30 °C to –40 °C, with summer mean monthly precipitation of 71 mm and snow covering the ground all winter (December to March).

The region has been subjected to logging and industrial mining for over 100 y. Environmental damage included approximately 20 000 ha of land rendered barren, and

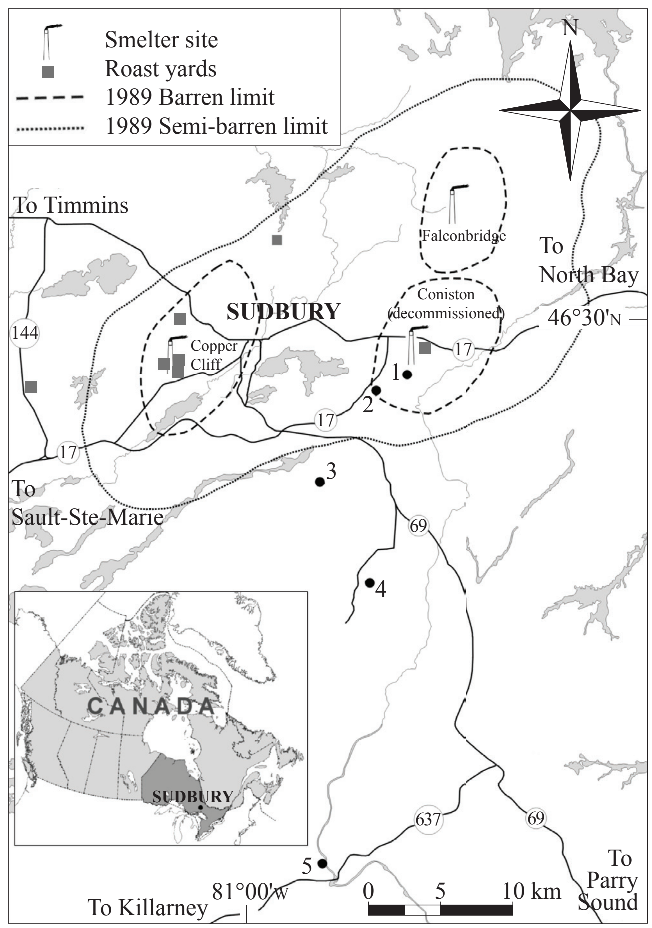

FIGURE 1. Map showing the location of the sites (black dots numbered 1 to 5) and the decommissioned smelter in Sudbury region, Ontario, Canada.

sulphur dioxide emissions and heavy metal deposits on vegetation, soil surface, and water had noticeable effects on sites within 40 km of the smelter (Gunn *et al.*, 1995). The smelter complex that generated the degradation was decommissioned in 1972, but because natural recovery of the forest is slow, the past stress gradient can be discerned on the landscape within about 40 km of the point source emissions (smelter). Differences in soil pH can still be found along the gradient of perturbation, with acidic soils in sites close to the smelter, and copper and nickel deposition decreases with increasing distance from the point source (Anand *et al.*, 2003).

Experimental design and data analysis

We performed experiments in 5 naturally recovering sites along the stress gradient at 2, 4, 12, 16, and 36 km from the decommissioned smelter (sites 1 to 5 respectively, Figure 1), with the closest site (2 km) being the most degraded (for more details of site characterization see Anand *et al.*, 2003; Rayfield, Anand & Laurence, 2005; and Babin-Fenske & Anand, 2011). Seed removal experiments were carried out simultaneously (June–July) in the 5 sites in 2010 and lasted 10 consecutive days. We chose seeds from 2 common plant species of the region using seed dispersal by fauna as their main dispersal syndrome and representing different vegetation layers (tree and herbaceous): acorns of red oak (*Quercus rubra*) and fruits of common blueberry (*Vaccinium angustifolium*). We use the term “seeds” in a broad sense to refer to plant propagules.

At each site, 10 feeding stations were arranged every 10 m in a 2 × 5 m grid. Each feeding station consisted of 3 metal dishes (10 cm diameter) with 10 blueberries and 5 acorns each. Within each feeding station, dishes differed in the way they were presented in order to identify if seeds were consumed by medium/big mammals (> 300 g), small mammals (< 300 g), or birds: a) medium/big mammal dishes were nailed to a tree, 30 cm above the ground; b) small mammal dishes were placed on the ground and protected with a 5-mm metallic mesh (50 × 50 × 10 cm^3) with 4 openings of 3 cm; and c) bird dishes were placed hanging from tree branches or between 2 trees, only available for flying vertebrates. As birds also had access to medium/big mammal dishes, the estimation of seed consumption for these dishes was done discounting the consumption made by birds in the same feeding station. Overall, 150 dishes were installed and visited every day to count and replace the seeds that were removed.

To quantify seed removal along the pollution gradient we calculated the regression coefficient between total percentage of seed removal and distance from smelter for the different types of seeds and dispersal vectors. To quantify vegetation structure we used extensive data on forest structure from the same sites from previous years. No significant changes in basal area of the forest occurred between 2006 and 2008 in the same sites (M. Anand, unpubl. data) and no major disturbances occurred in any of the sites since then, we used 2008 vegetation structure data. In all sites, vegetation was sampled on south-facing slopes using 2 parallel, 100-m transects that crossed natural gradients related to topography. Also, one 100-m transect perpendicular to the topography gradient was sampled. In each transect, understory vegetation cover was estimated using the Braun–Blanquet method in 1 × 1 m contiguous quadrats. We determined the density and diameter at breast height (DBH) of overstory trees in 5 × 5 m contiguous quadrats. From the understory data we determined total species cover and blueberry percentage cover. For overstory vegetation both basal area per hectare and red oak basal area per hectare were estimated.

To estimate direct and indirect causal relationships between vegetation variables and seed consumption, we used path analysis, a type of structural equation modelling (SEM) (Kline, 2005). Structural equation modeling is useful for partitioning the relative strengths of direct and indirect effects of 1 variable on another and is widely used in ecological studies. The strength of a direct causal effect between 2 variables is represented by a path coefficient. We first identified the predictor variables that were correlated with one another and eliminated them from the analysis (Kline, 2005). Then, we developed 2 conceptual models, 1 general and 1 specific, regarding the relationship between vegetation structure, distance to the smelter, and seed removal. The general model considered only generic structural vegetation variables (understory cover and overstory basal area per hectare), while the specific model analyzed the relationship between species-level cover and seed removal. For example, when acorn removal was analyzed, the specific model included red oak basal area per hectare instead of total basal area per hectare. For both models, path coefficients and goodness of fit were estimated using maximum likelihood from the covariance (between variables) matrix included in each model. The null hypothesis implicit in the model-fitting procedure is that there are no differences between observed and predicted covariance matrices (Fox, online). We evaluated the significance of the models using the χ^2 test. In order to determine if seed removal was better explained by the general model or the specific model we used the Schwartz–Bayes information criterion (BIC) to select the best-fit model. All analyses were done with R statistical software, and the “sem” package was used for path analysis (Fox, online).

Results

Seed removal along the pollution gradient

We found an increasing trend of seed removal along the pollution gradient. Seed removal was lower in the most degraded site, closest to the smelter (mean of the 3 treatments = 0.59% for blueberries, 0.076% for acorns) and higher in the least stressed site, 36 km away from the smelter (blueberries = 50.79%, acorns = 51.92%) (Figure 2). This trend was found for both types of seeds and treatments (birds, small mammals, medium/big mammals) (Figure 2). Seed removal by small mammals (Figure 2; blueberries R^2 = 0.94 and acorns R^2 = 0.56, both P < 0.01) and medium/big mammals (Figure 2; blueberries R^2 = 0.87 and acorns R^2 = 0.47, both P < 0.05) was positively correlated with increasing distance to smelter. On the other hand, seed removal by birds did not show a significant relationship with the pollution gradient (Figure 2; blueberries R^2 = 0.32 and acorns R^2 = 0.79, both P > 0.05). In site 4 (16 km away from the smelter), seed removal was as low as in the closest sites, for both seeds and the 3 dispersal vectors (Figure 2) even though forest structural parameters were similar to those of site 5 (36 km away from the smelter) (Table I).

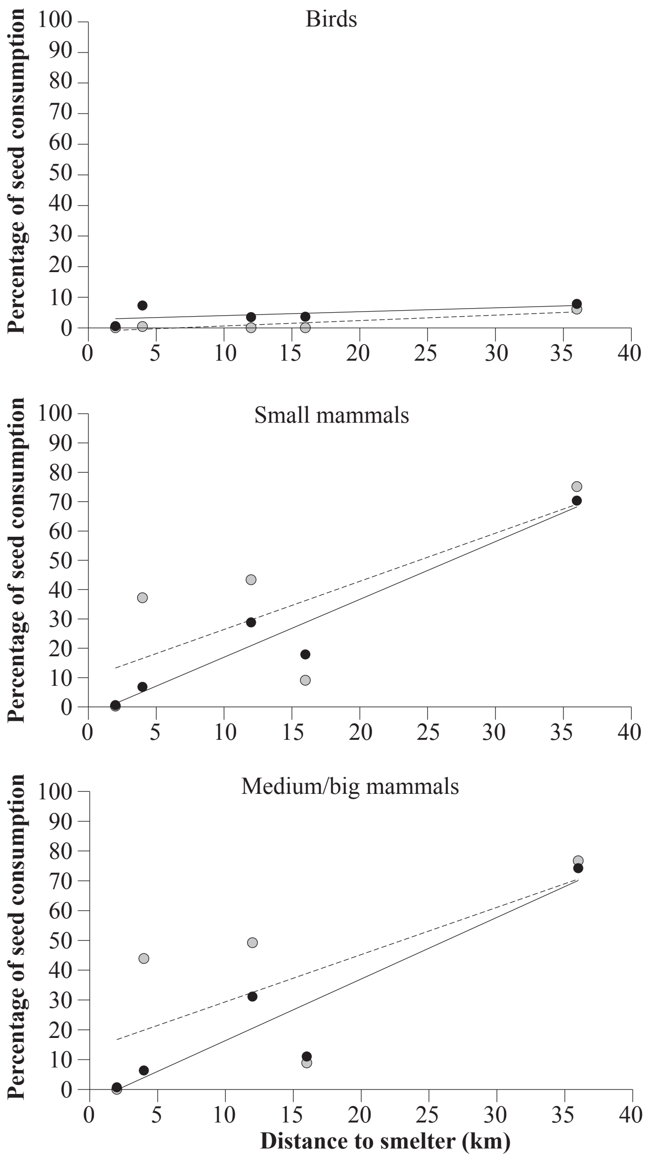

FIGURE 2. Mean percentage of seed removed along the pollution gradient. Black circles and solid lines are blueberry consumption values and regression trend. Grey circles and dashed lines are acorn consumption values and regression trend.

TABLE I. Measures of vegetation structure along the pollution gradient. Sites 1 to 5 represent increasing distance to smelter (shown in parentheses). Asterisks represent significant regression values (*$P < 0.05$; **$P < 0.01$).

	Basal area/hectare	Red oak basal area/hectare	Understory mean % cover	Blueberry mean % cover
Site 1 (2 km)	0.25**	0.00	32.52*	1.32*
Site 2 (4 km)	2.09**	0.12	58.07*	7.54*
Site 3 (12 km)	6.86**	0.74	84.59*	20.95*
Site 4 (16 km)	12.74**	1.41	82.53*	23.44*
Site 5 (36 km)	21.66**	1.09	82.24*	5.04*

VEGETATION STRUCTURE THROUGH THE POLLUTION GRADIENT

Out of 17 species present in site 1 (closest to the smelter), 4 comprised 89.7% of the understory cover: 2 non-vascular species (*Pohlia nutans* = 41.3% and *Polytrichum juniperinum* = 22.7%), 1 tree sapling (*Betula papyrifera* = 21.7%), and common blueberry (*Vaccinium angustifolium* = 4.06%). In site 2, understory cover was dominated by 6 species (53.54%): *Polytrichum strictum* = 1.8%, *B. papyrifera* = 3.77%, *P. nutans* = 4.04%, *V. angustifolium* = 7.53%, *Deschampsia flexuosa* = 9.43%, and *P. juniperinum* = 25.71%. In site 3, 7 species comprised 59% of understory cover, while in site 4, 6 species comprised 60.4% of the cover. In both sites, the common blueberry *V. angustifolium* was the dominant species (20.95% and 23.44% in site 3 and 4, respectively). In site 5, 11 species represented 60% of understory cover, with common blueberry ranking sixth (5.03%). Regarding overstory composition, only *B. papyrifera* was present in site 1. Among the 4 tree species present in site 2 (*B. papyrifera*, *Acer rubrum*, *Quercus rubra*, and *Pinus resinosa*), red oak was the third most abundant. A fifth woody species was present in site 3 (*Alnus viridis*), and 9 woody species were present in site 4; red oak was the third most abundant tree in both of these sites as well. Site 5 had 12 species, with *Corylus cornuta* being the most abundant and red oak the fifth most abundant.

Vegetation structure showed an increasing trend with increasing distance to point source of past pollution (Table I). Both general measures of vegetation structure showed positive and significant linear regression values with distance (total basal area per hectare $R^2 = 0.95$, $P < 0.01$; understory cover $R^2 = 0.85$, $P < 0.05$). Red oak basal area per hectare did not result in significant regression values ($R^2 = 0.81$, $P > 0.05$), but blueberry cover did show significant quadratic regression values with distance ($R^2 = 0.87$, $P < 0.05$).

SEED REMOVAL AND VEGETATION STRUCTURE RELATIONSHIP

Path models of best fit are shown in Figure 3. Seed removal by birds was not statistically significant, showing that no analyzed variable explained the observed pattern. For mammal seed consumption, the pattern depended on the type of seed analyzed. For blueberry consumption a specific path model best fit both small and medium/big mammal consumption patterns, but blueberry cover was not the variable that best explained the pattern of seed consumption. Instead, it was determined mainly by distance to smelter and total basal area per hectare (Figure 3a,b). Finally, for acorn consumption the general hypothesized model presented the best fit, and total basal area per hectare was the variable that best explained acorn consumption (Figure 3c,d).

Discussion

We evaluated changes in seed removal as a surrogate of the seed dispersion/predation process and showed for the first time that the process is altered by past pollution-related impacts. In general we found that forest structure degradation negatively affects seed consumption, with significantly lower removal values occurring in the most damaged sites and an increasing trend with decreasing degradation. Moreover, habitat structure seems to affect the process more importantly than potential availability of food. Our results also show that different dispersal vectors (birds *versus* mammals) have different responses to degraded habitats, directly affecting the rate of seed removal, though these general trends did not differ between the types of seed analyzed.

As different species show different behaviours regarding activity and seed handling, it is important to know the identity of the main animal species of the region (Sivy *et al.*, 2011). According to Robitaille and Linley (2006), total mammal richness in our study area includes several species. Small mammals are eastern chipmunk (*Tamias striatus*), Gapper's red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), house mouse (*Mus musculus*), deer mouse (*Peromyscus maniculatus*), short-tailed shrew (*Blarina brevicauda*), and masked shrew (*Sorex cinereus*). Rodents (the dominant group in small mammal assemblages) are known to mainly predate on seeds (Hulme, 1998), but eastern chipmunks have a scatter-hoarding behaviour with potential seed dispersal. With this potential mixed assemblage, seed removal by small mammals may indicate mainly seed predation, although dispersal is also a potential fate of seeds. For medium/big size mammals in the Sudbury region, the species assemblage may be composed of red squirrel (*Tamiasciurus hudsonicus*) and northern flying squirrel (*Glaucomys sabrinus*), both of which have scatter-hoarding behaviour, and red fox (*Vulpes vulpes*) and raccoons (*Procyon lotor*), both of which are considered opportunistic seed consumers (Lotze & Anderson, 1979; Lariviere & Pasitschniak-Arts, 1996; Robitaille & Linley, 2006). Regarding birds, we sighted blue jays (*Cyanocitta cristala*), which are known to disperse acorns in fragmented landscapes (Johnson *et al.*, 1997). Nevertheless, the lack of information about bird species richness in the region prevents us from inferring

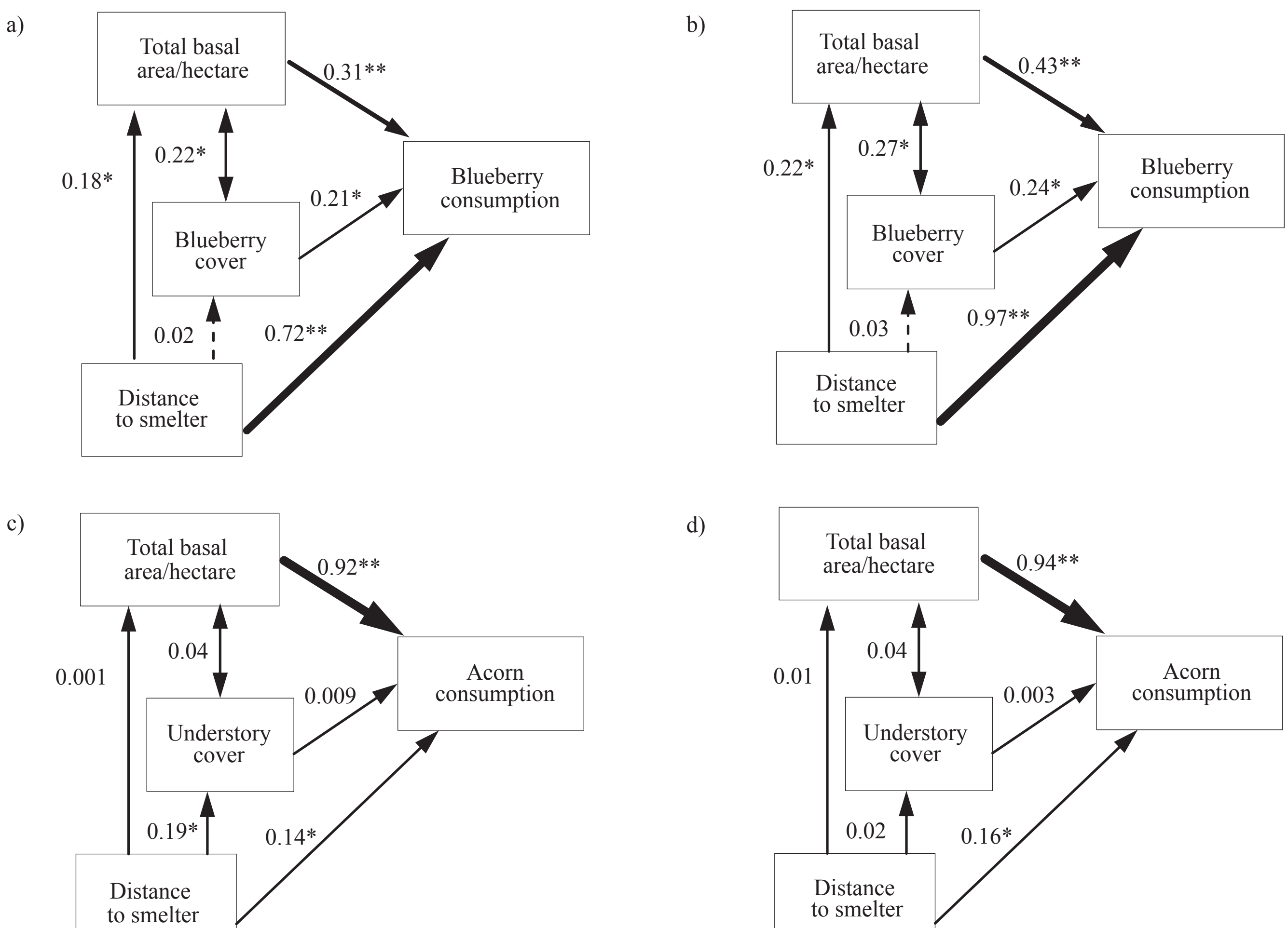

FIGURE 3. Path diagram representing the causal relationship obtained from the SEM analysis between forest structure, distance to smelter, and seed removal. Arrows show the causal relationship, and the thickness of the arrow represents the strength of the relationship. Continuous lines indicate positive effects; dashed lines indicate negative effects. One-headed arrows are directional effects, and two-headed arrows represent correlations between pairs of variables. Numbers next to each arrow are the partial correlation coefficients (*P < 0.05; **P < 0.01). Only best-fit models (lowest BIC) and those significantly different from null model (P > 0.05) are shown. a) blueberry consumption by small mammals (χ^2 = 27.7, P = 0.18); b) blueberry consumption by medium/big mammals (χ^2 = 24.6, P = 0.13); c) acorn consumption by small mammals (χ^2 = 15.5, P = 0.27); d) acorn consumption by medium/big mammals (χ^2 = 12.4, P = 0.3).

the potential composition of seed predators or dispersal along the gradient. The Sudbury Area Risk Assessment report (2009), however, suggests that the diversity of birds in the area is very low due to the effects of past pollution.

It is already known that changes in habitat structure affect faunal composition mainly through changes in food and refuge availability (Lassau & Hochuli, 2004; Tews *et al.*, 2004; among many others), but it is less well understood how those changes in richness and abundance affect the processes in which animals are involved (Herrera & García, 2010). Lack of research on the relationship between structural and functional components of the system limits our understanding of the dynamics of ecosystems, and in the particular case study presented here it may interfere with forest restoration and conservation efforts. For example, a positive relationship between tree basal area per hectare and site-specific mammal richness was found in Sudbury (Robitaille & Linley, 2006), which may indicate the presence but not the activity of fauna. With our results we were able to show that total basal area per hectare is among the most important variables influencing mammal consumption of blueberries and acorns.

When comparing between habitat (generic model) and food availability (specific model), path analysis shows that forest structure was more important in determining the amount of seed removal. For example, the specific model considering blueberry cover better explained blueberry removal, but within it, overstory structure had a stronger influence. Also, acorn removal was better explained with the generic model of overstory and understory structure as predictor variables. Moreover, our results show extremely low total seed removal in the site closest to the smelter. In this site, although blueberries were among the most common plant species, they were not more abundant than in the other sites. Thus, the lack of blueberry consumption could not be influenced by the availability in the surroundings. Rather, this may reflect low abundance of fauna and/or almost no activity in degraded habitats (*i.e.*, open patches are not used to feed). For animal prey species (the most abundant in our potential assemblages), predation risk is among the main limiting factors influencing their activity, and this risk is known to be lower in more complex habitats (Tews *et al.*, 2004; Whittingham & Evans, 2004; Sivy *et al.*, 2011). This may imply that forest quality (overstory structure, age of the stand, etc.) could be a determinant for animal activity. It has been suggested that increasing fruiting plants in a landscape could increase seed dispersal to early successional patches (Herrera & García, 2010). In light of our results we also suggest that increasing forest structure could be used as a first approach to increase animal activity and thus potential seed dispersal.

Our observation of low seed removal by birds in every site deserves special attention. Birds are known to be long-distance dispersal vectors and to play a key role in fragmented forest regeneration (Johnson *et al.*, 1997; García, Zamora & Amico, 2010). Thus, low seed removal by birds in all sites may indicate a serious limitation for long-distance seed dispersal, diminishing the connection of the more degraded sites with the less disturbed forest matrix. Due to the lack of published research on birds in the area, the reason for the low activity remains uncertain. Scheuhammer (2003) proposed that birds may be indirectly affected by acidification (due to past smelter emissions) through decreased availability of dietary calcium. This could affect birds' reproduction, reducing population abundance and thus causing low seed removal by birds in all sites. Also, the lack of bird-related seed removal may be related to our field methodology (*e.g.*, metal dishes could have caused rejection), and other studies that use diverse methods should be conducted.

Site 4 (16 km from the smelter) had an unusually low amount of seed consumption. The only detectable difference was the presence of the invasive orange-banded arion slug, *Arion fasciatus*, which merits further discussion. During the 10 d of the experiment we found several slugs in every dish, eating the blueberries and leaving mucus all over the acorns. This mucus is known to act as a defence against predation (Pakarinen, 1994), and it may also help to repel potential food competitors. Although native to Northern Europe, *A. fasciatus* spread to North America's cool wet climates, presumably during human colonization, and today it is considered a common pest slug. This slug has a generalist diet, being able to eat animal material, leaves, and detritus (Jennings & Barkham, 1975). Some species of the genus *Arion* have been found to disperse and even diminish predatory effects on geophyte seeds (Türke *et al.*, 2010), while others are known to diminish plant diversity in early successional stages and to profit from anthropogenic disturbance in forests (Buschmann *et al.*, 2005; Kappes, 2006). Further research is needed to corroborate the hypothesis that the slugs are the cause of low seed removal in site 4, and we consider this of urgent need due to the potential negative effect of invasive species on several ecosystem processes (Chapin *et al.*, 2000).

The results of this study highlight the importance of considering both structural and functional components of ecosystems when analyzing forest recovery from past pollution. We found that 40 y since pollution abatement is not enough time to recover structure and function in the most degraded habitats in our study site. These results contradict suggestions made by Jones and Schmitz (2009), who found that "ecosystem function" and "animal communities" recover more quickly than plant communities in forests. The need for more research on the relationship between structure and function of ecosystems recovering from degradation is compelling, and we hope our findings add to this research direction.

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Literature cited

Anand, M. & R. E. Desrochers, 2004. Quantification of restoration success using complex systems concepts and models. Restoration Ecology, 12: 117–123.

Anand, M., S. Laurence & B. Rayfield, 2005. Diversity relationships among taxonomic groups in recovering and restored forests. Conservation Biology, 19: 955–962.

Anand, M., K. Ma, A. Okonski, S. Levin & D. McCreath, 2003. Characterising biocomplexity and soil microbial dynamics along a smelter-damaged landscape gradient. Science of the Total Environment, 311: 247–259.

Babin-Fenske, J. & M. Anand, 2011. Patterns of insect communities along a stress gradient following decommissioning of a Cu–Ni smelter. Environmental Pollution, 159, doi: 10.1016/j.envpol.2011.04.011

Bennett, E. & P. Balvanera, 2007. The future of production systems in a globalized world. Frontiers in Ecology and Environment, 5: 191–198.

Buschmann, H., M. Keller, N. Porret, H. Dietz & P. J. Edwards, 2005. The effect of slug grazing on vegetation development and plant species diversity in an experimental grassland. Functional Ecology, 19: 291–298.

Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, S. Lavorel, H. L. Reynolds, D. U. Hooper, O. E. Sala, S. E. Hobbie, M. C. Mack & S. Diaz, 2000. Consequences of changing biodiversity. Nature, 405: 234–242.

Farwig, N., B. Bleher, S. von der Gönna & K. Böhning-Gaese, 2008. Does forest fragmentation and selective logging affect seed predators and seed predation rates of *Prunus africana* (Rosaceae)? Biotropica, 40: 218–224.

Forget, P.-M., P. Jordano, J. Lambert, K. Böhning-Gaese, A. Traveset & S. J. Wright, 2011. Frugivores and seed dispersal (1985–2010): The 'seeds' dispersed, established and matured. Acta Oecologica, 37: 517–520.

Fox, J. sem: Structural Equation Models Package. Online [URL] http://cran.r-project.org/web/packages/sem/index.html (Accessed on 10 May 2012).

García, D. & N. P. Chacoff, 2007. Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. Conservation Biology, 21: 400–411.

García, D., R. Zamora & G. C. Amico, 2010. Birds as suppliers of seed dispersal in temperate ecosystems: Conservation guidelines from real-world landscapes. Conservation Biology, 24: 1070–1079.

Gunn, J., W. Keller, J. Negusanti, R. Potvin, P. Beckett & K. Winterhalder, 1995. Ecosystem recovery after emission reductions: Sudbury, Canada. Water, Air, & Soil Pollution, 85: 1783–1788.

Herrera, M. & D. García, 2010. Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conservation Biology, 24: 1089–1098.

Hulme, P. E., 1998. Postdispersal seed predation: Consequences for plant demography and evolution. Perspectives in Plant Ecology, Evolution and Systematics, 1: 46–60.

International Commission on Zoological Nomenclature, online. Standards, sense, and stability for animal names in science. London, UK. Online [URL] http://iczn.org (Accessed on 10 September 2010).

Jennings, T. J. & J. P. Barkham, 1975. Food of slugs in mixed deciduous woodland. Oikos, 26: 211–221.

Johnson, W. C., C. S. Adkinsson, T. R. Crow & M. D. Dixon, 1997. Nut caching by blue jays (*Cyanocitta cristata* L.): Implications for tree demography. American Midland Naturalist, 138: 357–370.

Jones, H. & O. Schmitz, 2009. Rapid recovery of damaged ecosystems. PLoS ONE, 4: e5653, doi: 10.1371/journal.pone.0005653

Kappes, H., 2006. Relations between forest management and slug assemblages (Gastropoda) of deciduous regrowth forests. Forest Ecology and Management, 237: 450–457.

Kataev, G. D., J. Suornela & P. Palokangas, 1994. Densities of microtine rodents along a pollution gradient from a copper–nickel smelter. Oecologia, 97: 491–498.

Kline, R. B., 2005. Principles and Practice of Structural Equation Models. 2nd Edition. Guilford Press, New York, New York.

Kozlov, M. V. & E. L. Zvereva, 2007. Industrial barrens: Extreme habitats created by non-ferrous metallurgy. Review of Environmental Science and Biotechnology, 6: 231–259.

Kozlov, M. V. & E. L. Zvereva, 2011. A second life for old data: Global patterns in pollution ecology revealed from published observational studies. Environmental Pollution, 159: 1067–1075.

Lariviere, S. & M. Pasitschniak-Arts, 1996. *Vulpes vulpes*. Mammalian Species, 537: 1–11.

Lassau, S. A. & D. F. Hochuli, 2004. Effects of habitat complexity on ant assemblages. Ecography, 27: 157–164.

Leithead, M., Anand, M. Duarte, L. & Pillar, V., 2012. Causal effects of latitude, disturbance and dispersal limitation on richness in a recovering temperate, subtropical and tropical forest. Journal of Vegetation Science, 23: 339–351.

Lotze, J. H. & S. Anderson, 1979. *Procyon lotor*. Mammalian Species, 119: 1–8.

Newmaster, S. G. & S. Ragupathy, online. Flora Ontario – Integrated Botanical Information System (FOIBIS), Phase 1. University of Guelph, Canada. Online [URL] http://www.uoguelph.ca/foibis/ (Accessed on 10 September 2010).

Pakarinen, E., 1994. The importance of mucus as defence against Carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum*. Journal of Mollusc Studies, 60: 149–155.

Perner, J., W. Voigt, R. Bährmann, W. Heinrich, R. Marstaller, F. Bärbel, G. Karsten, D. Lichter, F. W. Sander & T. H. Jones, 2003. Responses of arthropods to plant diversity: Changes after pollution cessation. Ecography, 26: 788–800.

Rayfield, B. & M. Anand, 2005. Assessing simple *versus* complex restoration strategies for industrially disturbed forests. Restoration Ecology, 13: 639–650.

Robitaille, J. & R. D. Linley, 2006. Structure of forests used by small mammals in the industrially damaged landscape of Sudbury, Ontario, Canada. Forest Ecology and Management, 225: 160–167.

Scheuhammer, A. M., 2003. Effects of acidification on the availability of toxic metals and calcium to wild birds and mammals. Environmental Pollution, 71: 329–375.

Sivy, K. J., S. M. Ostoja, E. W. Schupp & S. Durham, 2011. Effects of rodent species, seed species, and predator cues on seed fate. Acta Oecologica, 37: 321–328.

Sudbury Area Risk Assessment (SARA) Group. Volume III, Chapter 4: Wildlife. Online [URL] http://www.sudburysoilsstudy.com/EN/indexE.htm (Accessed on 20 October 2010).

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager & F. Jeltsch, 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography, 31: 79–92.

Türke, M., E. Heinze, K. Andreas, S. A. Svendsen, M. M. Gossner & W. W. Weisser, 2010. Seed consumption and dispersal of ant-dispersed plants by slugs. Oecologia, 163: 681–693.

Willson, M. & A. Traveset, 2000. The ecology of seed dispersal. Pages 85–110 *in* M. Fenner (ed.). Seeds: The Ecology of Regeneration in Plant Communities. 2nd Edition. CAB International, Wallingford.

Whittingham, M. J. & L. Evans, 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis, 146: 210– 220.

Wunderle, J. M., Jr., 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management, 99: 223–235.

Zvereva, E. L., E. Toivonen & M. V. Kozlov, 2008. Changes in species richness of vascular plants under the impact of air pollution: A global perspective. Global Ecology and Biogeography, 17: 305–319.