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Influence of canopy cover and amount of open habitat in the surrounding landscape on proportion of alien plant species in forest sites[1]

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Abstract: Most alien plant species are open-habitat species. Therefore, at the site scale, canopy openness should favour the germination and growth of alien species, and at the landscape scale the presence of open habitat should increase the seed rain and therefore the colonization rate of forest sites by alien species. We tested these two hypotheses by quantifying the proportion of alien understory plant species in 192 forest sites ranging in canopy cover and amount of open habitat in the surrounding landscapes. Our results supported both hypotheses, although the total amount of variance explained was low (12%). The proportion of alien plant species in forest sites increased with decreasing canopy cover at the site and with increasing amount of open habitat in the landscapes surrounding the forest sites. The effect of canopy cover was much stronger than the effect of amount of open habitat in the surrounding landscapes, suggesting that conditions for germination and growth are a stronger limitation on alien species incursion into these forest sites than is the availability of alien species propagules.
Keywords: alien species, canopy cover, colonization, exotic species, germination, herbaceous plants, invasion, invasive species, landscape context, matrix, non-native species, old-field, open habitat, seedling.

Résumé : La plupart des plantes exotiques colonisent les milieux ouverts. Par conséquent, à l'échelle d'un site, l'ouverture de la voûte forestière devrait favoriser la germination et la croissance de ces espèces. À l'échelle du paysage, la quantité de milieux ouverts devrait accroître la dissémination des graines d'espèces exotiques ainsi que le taux de colonisation des sites forestiers par ces espèces. Nous avons vérifié ces deux hypothèses en quantifiant la proportion d'espèces végétales exotiques dans le sous-bois de 192 sites forestiers avec voûte forestière plus ou moins fermée et dont les paysages avoisinants renferment une plus ou moins grande quantité de milieux ouverts. Les résultats obtenus confirment les deux hypothèses, bien que la variance totale expliquée soit faible (12 %). La proportion d'espèces exotiques dans les sites forestiers augmente avec l'ouverture de la voûte au niveau du site et avec l'accroissement des habitats ouverts dans les paysages entourant les sites. L'effet du couvert forestier est plus grand que celui de la quantité de milieux ouverts dans les paysages avoisinants, ce qui suggère que les conditions de germination et de croissance soient plus limitatives pour l'établissement des plantes exotiques que la disponibilité des diaspores de ces plantes.
Mots-clés : champ en friche, colonisation, contexte du paysage, espèces envahissantes, espèces exotiques, germination, invasion, matrice, milieu ouvert, plantes herbacées, plantule, voûte forestière.

Nomenclature: Gillett, 1958; Fernald, 1970; Niering & Olmstead, 1979; Preston, 1989; Soper & Heimburger, 1994; Chambers *et al.*, 1996.

Introduction

Most alien plant species are open-habitat species, probably because most introductions have occurred through agriculture and gardening (Cowie & Werner, 1993; Fensham & Cowie, 1998; Cadotte & Lovett-Doust, 2001; Weaver, Gustafson & Lichthardt, 2001; Rubino, Williams & Moriarity, 2002). Several authors have therefore suggested that forest sites with a more open canopy should be more likely to contain alien species; such species should germinate and grow more readily in open micro-sites within the forest than in micro-sites with a closed canopy (Brothers & Spingarn, 1992; Meekins & McCarthy, 2001; Meiners, Pickett & Cadenasso, 2002).

In addition, forest sites that are situated in a landscape context dominated by open habitats, primarily agricultural fields, should receive more alien plant seeds than forest sites situated in landscapes containing more continuous forests. The higher abundance of alien plants in landscapes containing more open habitats should result in a larger influx of seeds of alien plant species into forest patches within these landscapes (Boutin & Jobin, 1998; Cullen *et al.*, 2001; Meekins & McCarthy, 2001).

Therefore, habitat openness is predicted to increase the prevalence of alien species in forest sites via two mechanisms operating at two scales. At the site scale, canopy openness should favour the germination and growth of alien species, and at the landscape scale the presence of open habitat should increase the seed rain and therefore the colonization rate of forest sites by alien

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species. In this study we tested these two hypotheses by quantifying the proportion of alien understory plant species in 192 forest sites ranging in canopy cover and amount of open habitat in the surrounding landscapes.

Methods

Twenty-nine 1-km^2 landscapes, each containing 10 randomly distributed vegetation sampling sites, were established by T. Contreras in the Ottawa-Carleton region (~ 2,900 km^2) in 1997 to study the effects of forest cover on propagation of wind-dispersed *versus* animal-dispersed plants. The landscapes were chosen to represent a wide range in forest cover (range: 1% to 93%). One hundred and ninety-two of the 290 sites were forest sites, and the remaining 98 were in fencerows and old fields. Important for the current study, the 192 forest sites represented a wide range of canopy cover (sites ranged from 17% to 97% cover) and a wide range in amount of open habitat in the surrounding landscapes (from 0% to 99% open habitat within a 500-m radius). In addition, these two variables were uncorrelated (r = -0.02, P = 0.79), so we could estimate their independent effects on alien species occurrence in the forest sites.

In Contreras' study (Contreras, 2002), each vegetation sampling site was a 25-m × 12.5-m tree-sampling plot containing a nested 12.5-m × 6.25-m shrub-sampling plot. Each shrub plot contained two 1-m^2 quadrats, which were 10.5 m apart (at the northwest and southwest corners of the shrub plots), for sampling seedlings and herbaceous understory vegetation. The long axis of each site was aligned in a north-south orientation with the exception of sites in fencerows, which were aligned with fencerow orientation. Sites were located on fairly flat terrain (0° to 22°) except for one site on a hillside and one site along a ravine (slope of 45° and 39°, respectively). Most soil in the study region is of a loamy texture, but soils in the eastern part of the region are wetter and have higher clay content, lower litter thickness, deeper organic horizons, and woodier litter than soils in the western part.

Forest sites were located in mixed-age forest stands. Dominant canopy species shift from *Acer saccharum* in the western portion of the study region to *Fraxinus* sp., *Populus tremuloides*, and *Ulmus* sp. in the eastern portion. *Pinus strobus*, although not as prevalent as *A. saccharum* across the whole region, was often the most dominant species where it did occur. In addition, *Ostrya virginiana* was often a predominant intermediate species.

In the summer of 1999 we re-sampled the understory quadrats. Seedlings and herbaceous ground vegetation species were identified, in most cases to species, and were categorized as either alien (*i.e.,* introduced to the Ottawa-Carleton region, in most cases from Europe) or native (Gillett, 1958; Fernald, 1970; Niering & Olmstead, 1979; Preston, 1989; Soper & Heimburger, 1994; Chambers *et al.,* 1996). Plants not identifiable to species and belonging to genera containing native and alien species in the study region were eliminated from the dataset. At each site, we determined the percentage of species that were alien in the two 1-m^2 quadrats (combined).

We used a canopy-quantification method similar to that of James and Shugart (1970). Observations were made with a vertical sight tube every 2 m, for 10 m along each of four cardinal directions, from the midpoint between each pair of quadrats (Contreras, 2002). The number of positive readings out of 40 was taken as the canopy-cover index at each site.

Digitized topographic maps (National Topographic Data Base, Geomatics Canada) at 1:50,000 scale in MapInfo format (MapInfo Corp., Troy, New York, USA) of forest cover, wetland cover, and water bodies (rivers and lakes) for the Ottawa-Carleton region (1997 topographic maps 31F/1, 31F/8, 31G/3, 31G/4, 31G/5, 31G/6) were converted to ArcView 3.2 format (Environmental Systems Research Institute, 1996). The percentage of open habitat (*i.e.,* all areas not including forest, wetland, or water bodies) within 200 m, 500 m, 1,000 m, and 2,000 m of all forest sites was quantified using Patch Analyst 2.1 and the Avenue script calcapl.ave.

First, we tested our assumption that alien plant species are more prevalent in open habitats, by comparing mean percentage of alien species in forest sites *versus* open-habitat sites (old fields and fencerows). We then determined the spatial scale at which the amount of open habitat in the landscape was most strongly related to the percentage of species that were alien, by calculating the correlation between these two variables at each of the four buffer distances. Finally, we conducted a multiple regression analysis of the percentage of species that were alien on the amount of open habitat in the landscape (at the scale identified) and the canopy cover of the site. The response variable was first arcsin square-root transformed.

Results

In all, 325 plant species were sampled, of which 65 were alien. There was a much higher mean (± SE) percentage of alien species in open habitat sites (43.25 ± 2.05%) than in forest sites (8.54 ± 0.92%; t = -15.4, P < 0.0001).

The percentage of species in forest plots that were alien was most strongly correlated with surrounding open habitat within 200 m of the forested sites. In the multiple regression model, canopy cover and open habitat were both significant predictors of the percentage of alien species, explaining 12% of the variation. Canopy cover was the stronger predictor in the model; on average, sites with more canopy had fewer alien species (standardized regression coefficient = -0.095; partial r^2 = 0.09; P < 0.0001). On average, sites with more open habitat in the surrounding landscapes (within 200 m) contained more alien species (standardized regression coefficient = 0.012; partial r^2 = 0.027; P = 0.017). Both relationships were very weak (Figures 1 and 2).

Discussion

Our results supported both our initial hypotheses. The proportion of alien plant species in forest sites increased with decreasing canopy cover at the site; this supports the hypothesis that germination and growth of alien species in forest sites is facilitated by canopy openness. The propor-

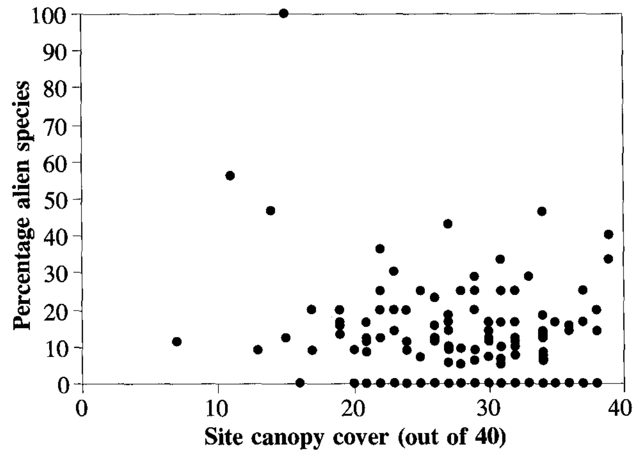

FIGURE 1. Percentage of species of herbaceous plants and woody seedlings that were alien species as a function of site canopy cover, in 192 forest sites.

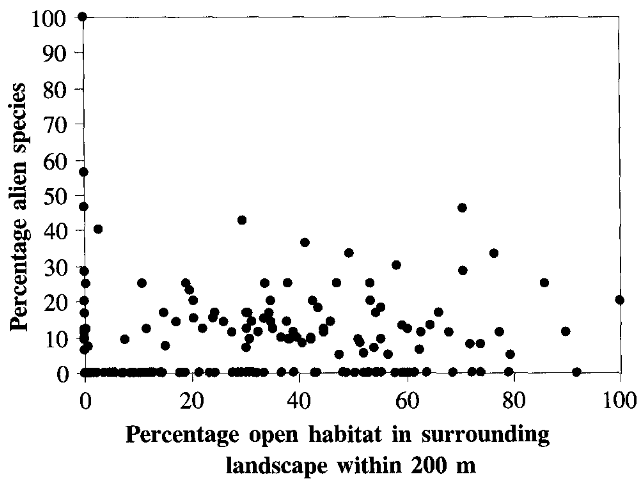

FIGURE 2. Percentage of species of herbaceous plants and woody seedlings that were alien species as a function of the amount of open habitat in the landscapes surrounding the sites (within 200 m), in 192 forest sites.

tion of alien plant species in forest sites also increased with increasing amount of open habitat in the landscapes surrounding the forest sites; this supports the hypothesis that colonization of forest sites by alien plant species is higher in landscapes containing more open habitat. Several other studies have shown an increase in the abundance or species richness of alien plants with decreasing canopy cover (Hutchinson & Vankat, 1997; McNab & Loftis, 2002; Teo *et al.*, 2003). However, as far as we are aware, ours is the first study to test the hypothesis that the amount of open habitat in the surrounding landscapes influences the number of alien plant species in forest sites.

Since canopy cover and amount of open habitat within 200 m of the sites were not correlated ($r = -0.02$, $P = 0.79$), we were able to evaluate the relative effects of these two variables on the proportion of species that were alien. The effect of canopy cover was about an order of magnitude stronger than the effect of amount of open habitat in the landscapes, even though the range of values of open habitat was slightly larger (0-99%) than the range of values of canopy cover (17-97%) in our study. Therefore, we conclude that alien plant species distribution in forest sites in our region is more strongly limited by canopy openness than by seed availability.

However, 88% of the total variation in proportion of alien species was not explained by the predictor variables we studied. Site variables such as soil characteristics, slope aspect, elevation, windiness, soil pH, amount of coarse woody debris, ground cover, and site productivity may explain some of the remaining variability (McNab & Loftis, 2002; Kupfer & Runkle, 2003; Teo *et al.*, 2003). Even if the effects of all these site variables were accounted for, it is likely that the amount of unexplained variation would remain large. Chance events and differences in the history of the sites, particularly the human use and disturbance history, likely explain a large portion of the variation in alien plant species distributions (Stansbury & Scott, 1999; Kupfer & Runkle, 2003; Pysek, Jarosik & Kucera, 2003).

In summary, our results support the hypotheses that *i*) alien species are more likely to germinate and grow in forest sites with more open canopies and *ii*) forest sites in landscapes containing more open habitat receive a larger seed rain of alien plant species. The effect of canopy cover was much stronger than the effect of amount of open habitat in the landscape, suggesting that conditions for germination and growth are a stronger limitation on alien species incursion into forest sites than is the availability of alien species propagules.

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