Ecological and taxonomic differences between native and introduced plants of southwestern Ontario

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Abstract: We compared taxonomic and ecological attributes of native and introduced plants (N = 1330 and 484 species, respectively) of southwestern Ontario, using two regional floras (Essex County and Hamilton-Wentworth Regional Municipality) for distributions, and published sources for ecological attributes. Most exotics (86.4%) originate from Europe and Asia. Exotic species tended to occur in families having just one-to-few species locally. Seven families (Amaranthaceae, Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Fabaceae, and Malvaceae) were significantly over-represented by exotics compared to the distribution of native species in these families, while exotics were significantly under-represented in six families (Cyperaceae, Fagaceae, Juncaceae, Orchidaceae, Potamogetonaceae, and Ranunculaceae). In habitat comparisons, exotic species were significantly over-represented (compared to native species) in disturbed and degraded habitats and moist substrates, while being under-represented in woodland, thicket, and wetland. Introduced species of southwestern Ontario have life history traits that facilitate success in degraded, disturbed and highly fragmented environments. For example, exotics were significantly over-represented by the following life-history traits: short life span, flowering season of four or more months, hermaphroditic sex habit, and very small fruits (< 5 mm). They were significantly under-represented by the monococious and dioecious sex habits, a flowering period of two months and less, animal-based seed dispersal, and relatively small fruits (5.1 - 10 mm). A separate analysis of exotic species found only in undisturbed communities, showed these species to be more likely to occur in open and moist habitats, to have a tree habit, and an extended flowering period, and to produce many seeds per fruit (> 7).

Keywords: invasiveness, exotic plants, comparative analyses, habitat change, life-history features.

Résumé : Nous avons comparé les caractéristiques taxonomiques et écologiques d’espèces de plantes indigènes (N = 1330) et introduites (N = 484) du Sud-Ouest de l’Ontario. Les informations sur la répartition des espèces ont été colligées dans deux floras régionales (celles du comté d’Essex et de la municipalité régionale d’Hamilton-Wentworth). Les informations sur les caractéristiques écologiques des espèces ont été trouvées dans d’autres publications. La plupart des espèces exotiques (86.4 %) proviennent d’Europe et d’Asie. Les espèces exotiques se trouvent surtout dans les familles qui ne comptent qu’un petit nombre d’espèces dans une même localité. Sept familles (Amaranthaceae, Astereaceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Fabaceae et Malvaceae) sont significativement sur-représentées par les espèces exotiques par rapport aux espèces indigènes. Six autres familles sont au contraire sous-représentées (Cyperaceae, Fagaceae, Juncaceae, Orchidaceae, Potamogetonaceae et Ranunculaceae). Les espèces exotiques sont sur-représentées dans les habitats perturbés et dégradés et sur substrat humide, alors qu’elles sont sous-représentées dans les boisés, les fougères et les terres humides. Les espèces introduites du Sud-Ouest de l’Ontario ont des caractéristiques qui facilitent leur établissement dans les environnements perturbés, dégradés et très fragmentés. Par exemple, les espèces exotiques dont la durée de vie des individus est courte, dont la période de floraison s’étend sur quatre mois ou plus, qui sont hermaphrodites et qui produisent de petits fruits (< 5 mm), sont significativement sur-représentées dans les assemblages d’espèces. Par contre, les espèces exotiques dont les individus ne portent que des fleurs d’un seul sexe, qui ont une floraison de courte durée (deux mois ou moins), qui dissèment leurs diaspores grâce aux animaux et qui produisent de plus gros fruits (5.1 - 10 mm), sont significativement sous-représentées dans les assemblages. Une analyse distincte des espèces exotiques trouvées uniquement dans les communautés non perturbées montre que ces espèces sont surtout présentes dans les habitats ouverts et humides. Elles ont aussi un port arborescent et une floraison prolongée, et leurs fruits contiennent beaucoup de graines.

Mots-clés : capacité d’invasion, plantes exotiques, analyses comparatives, changement d’habitat, caractéristiques du cycle vital.

Introduction

Ecologists have historically focused on two main questions with respect to plant invasiveness: the life history traits of successful invasive species, and the characteristics of communities that this tend to be susceptible to invasions (Baker, 1974; Moulton & Pimm, 1986; Noble, 1989; Pysek, Prach & Smilauer, 1995; Burke & Grime, 1996; Rejmanek, 1996; Rejmanek & Richardson, 1996; Lonsdale, 1999; Levine, 2000). Recent work has also attended to the role of taxonomy and phylogenetic influences on species invasiveness. For example, Pysek and others have considered whether particular families or orders are more prone than others to invasiveness (Pysek, Prach & Smilauer, 1995; Pysek, 1997a; Pysek, 1998a; Weber, 1997).

The issue is clearly complex, and early descriptive treatments, such as Baker's (1974) twelve characteristics of the "ideal" weed, have given way to comparative analyses (Williamson & Fitter, 1996). Many generalizations about invasive species have emerged from detailed studies that examine traits of individual, conspecific, or a limited number

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i) Climate in a taxon's place of origin must be similar to colonizing habitat.

ii) Invading taxa should be of similar life form to native taxa.

iii) Soils of place of origin should be similar.

iv) Invading taxa should have a generalized pollination (wind or general insect), or self-pollination system.

v) Invading taxa should have an appropriate dispersal system i.e., an ability to be mobile in a new habitat.

vi) The breeding system of an invader should allow for sexual reproduction at low densities (without inbreeding depression), but also be able to promote genetic variation through recombination (i.e., facultative apomixis or self-compatibility).

vii) Vegetative reproduction may be a very important trait for invasions in dense communities where native taxa rely on vegetative reproduction.

General conclusions in the literature are that exotic and invasive species in North America have benefitted from European colonization and trade, intense levels of disturbance regimes, and land-use expansion (especially agriculture and urban development (Baker, 1986; Given, 1994; Weber, 1997; Pysek, 1998b)). Regular disturbances, especially those found in agricultural landscapes, offer beneficial habitats (open space, reduced competition, or food resources) into which invading taxa can colonize and propagate (Orians, 1986, Pimentel, 1986). The establishment and spread of exotic species by landscape alteration is of major conservation concern. Indeed, following habitat loss, the spread of alien species is the single greatest threat to biodiversity in the U.S. (Wilcove et al., 1998).

Here we examine characteristics of the flora of southwestern Ontario, at the northern limit of the Mixed Wood Plains ecozone (Wiken, 1986). This study compares the frequency of selected traits in native and introduced species. In general, we examine whether native and introduced species differ with respect to origin, taxonomy, habitat preferences, and life history attributes. Specific hypotheses test the patterns detailed by Baker (1986), listed above.

**Material and methods**

The study region extends from the northern shores of Lake Ontario and Lake Erie (including the archipelago of Erie islands) to lower Lake Huron and the Detroit River, and is one of the most biologically diverse in Canada (Allen, Eagles & Price, 1990; Catling & Cayouette, 1996). It is of overriding conservation importance due to extreme pressures from human settlement and development, moreso than perhaps in any other region of Canada.

We compiled a database of native and introduced plants in southwestern Ontario, using two regional floras. Goodban (1993) included 1161 vascular plants from the Hamilton-Wentworth Regional Municipality, in southern Ontario. This was supplemented by a further 479 taxa (not occurring in Hamilton-Wentworth), from the flora of Essex County (Botham, 1981) in extreme southwestern Ontario. Origin of non-native species was taken from Scoggan (1978). Taxonomic designations follow Cronquist (1988). Growth habit and community associations were based on Gleason (1952). Gleason gave specific habitat associations from which we categorized general habitat preferences. For example, grassland, old field, prairie, and meadow habitat associations were grouped together as "open habitat", as a taxon's habitat association. (Gleason's full array of habitat types would have been problematic to analyze, with too fine a division of taxa among habitat types. It should also be noted that classifying taxa into habitat associations is not meant to imply that they are necessarily found in a single habitat; rather we sought to compare taxa on the basis of their typical or "preferred" habitat type.) Similarly, soil moisture preferences were based on Gleason's description of typical or optimal soil conditions. These were simply classified as dry, moist, or wet, or some combination of these.

Life history information (including growth habit, presence of clonal organ, life cycle, sex habit, flowering period, fruit size, and number of seeds per fruit) was taken from Gleason (1952). For other details not given by Gleason (such as mating system, method of seed dispersal and pollination syndrome) we searched the primary literature.

Sporne (1980) used 107 morphological and biochemical traits to rank dicotyledonous families with respect to numbers of retained traits, and generated an Advancement Index. We used Sporne's Advancement Index (Schwartz, 1993), to determine whether families containing an excess of exotic species in southwestern Ontario were among those that, comparatively, had either particularly retained, or lost 'primitive' characteristics.

The number of exotic species per family was compared (using linear regression) to patterns of global family size. Global family sizes were taken from Walter & Gillett (1998). Both global- and local-exotic family sizes were log-transformed because their distributions were significantly right-skewed (G/SES > 2: where G is skewness, and SES is the standard error of skewness; see SPSS, 1999).

Linear regression analysis was also used to examine the relationship between (log) number of exotic species per family and Sporne's Advancement Index for that particular family. Also, because there is an apparent lower ceiling in this data, we used a one-cycle partition regression (a two-cycle was not possible due to insufficiency of data points) as a method of explanatory data analysis (Thomson et al., 1996). Essentially, a one-cycle partition regression uses the first regression line to divide the data cloud into two halves, and separate second-ary regressions are performed on each half of the data cloud. This allows determination of any relationship following exclusion of the bottom ceiling in the data.

All other comparative analyses were carried out using χ² contingency analysis, with a Freeman-Tukey deviate test including a Bonferroni correction for multiple tests (Legendre & Legendre, 1998), to identify significantly over- and under- represented frequencies of life history attributes for native and exotic species. For any particular variable (habitat preferences, pollination syndrome, etc.) comparisons were carried out with only those taxa for which pertinent information was available; taxa for which
information was not available were excluded from that portion of the analysis. For example, habitat preferences were scored for 368 of the 484 exotic taxa, and therefore 116 taxa were excluded from analysis concerning habitat preferences. Where appropriate (i.e., 1 degree of freedom) Yates correction was carried out.

To examine possible interactions between habitat preference and life history attributes in introduced species (Noble, 1989; Pysek, 1997b), we separately distinguished those exotics found in disturbed sites from those found in undisturbed, natural communities and re-analyzed these using only exotics occurring in natural communities. Exclusions of taxa that occur in disturbed habitats were done based upon Gleason's (1952) classification of a taxon's typical habitat which, for disturbed habitats, Gleason referred to as disturbed, wasteland, urban, agricultural areas, and along roads and railway tracks.

Results

The two regional floras had a combined total of 1814 species of flowering plant. Of these, 1330 (72.9%) were native species (including 8 [0.4%] of unknown status) and 484 (26.7%) were introduced to Ontario. The majority of introduced species originated in Eurasia (63%), Western Europe (17.1%), and Asia (6.3%). Very few species originated in sub-tropical or tropical regions (3.8% Central and South America, Africa).

Taxonomic Patterns

Figure 1 shows that globally larger families were significantly more likely (P < 0.01) to be represented by larger families in the pool of exotic species. However, this relationship is relatively weak (R² = 0.35), suggesting that global family size is not the only important influence upon the number of exotic species per family.

Seven families were significantly over-represented by exotic species compared to the family patterns for native species (Amaranthaceae, Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Fabaceae, and Malvaceae), while six families appeared significantly under-represented by exotics (Cyperaceae, Fagaceae, Juncaceae, Orchidaceae, Potamogetonaceae, and Ranunculaceae; Table 1). The general pattern of family size appears similar for native and exotic species (Figure 2); both appear to have modes at monotypic families, and families that account for many of the taxa.

Table 1. Results of χ² contingency analysis of the frequency of species in families with at least one percent of native or introduced species of southwestern Ontario (* = significantly over-represented; underline = significantly under-represented; P < 0.05).

<table>
<thead>
<tr>
<th>Family</th>
<th>Introduced</th>
<th>Native</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaranthaceae</td>
<td>5*</td>
<td>1</td>
</tr>
<tr>
<td>Apiaceae</td>
<td>5</td>
<td>25</td>
</tr>
<tr>
<td>Aristolochiaceae</td>
<td>9</td>
<td>15</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>88*</td>
<td>134</td>
</tr>
<tr>
<td>Boraginaceae</td>
<td>13*</td>
<td>11</td>
</tr>
<tr>
<td>Brassicaceae</td>
<td>38*</td>
<td>25</td>
</tr>
<tr>
<td>Caprifoliaceae</td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td>22*</td>
<td>11</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td>9</td>
<td>12</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>4</td>
<td>167*</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>25*</td>
<td>30</td>
</tr>
<tr>
<td>Fagaceae</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Juncaceae</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>22</td>
<td>37</td>
</tr>
<tr>
<td>Liliaceae</td>
<td>14</td>
<td>37</td>
</tr>
<tr>
<td>Malvaceae</td>
<td>6*</td>
<td>3</td>
</tr>
<tr>
<td>Onagraceae</td>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>Orchidaceae</td>
<td>1</td>
<td>36</td>
</tr>
<tr>
<td>Poaceae</td>
<td>54</td>
<td>114</td>
</tr>
<tr>
<td>Potamogetonaceae</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td>4</td>
<td>33</td>
</tr>
<tr>
<td>Rosaceae</td>
<td>21</td>
<td>86</td>
</tr>
<tr>
<td>Salicaceae</td>
<td>11</td>
<td>21</td>
</tr>
<tr>
<td>Scrophulariaceae</td>
<td>14</td>
<td>33</td>
</tr>
<tr>
<td>Solanaceae</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Violaceae</td>
<td>4</td>
<td>21</td>
</tr>
<tr>
<td>Overall χ² = 214.64; P &lt; 0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. Relationship between global family size and the number of exotic species in family in southwestern Ontario (P < 0.01; R² = 0.35).

Figure 2. Frequency distribution of the number of introduced and native species per family in southwestern Ontario.
Linear regression analysis of Sporne’s Advancement Index (Figure 3) shows that neither families retaining more primitive traits nor those with fewer primitive traits were over-represented among exotic species \((R^2 = 0.001; P = 0.651)\). Using this regression as the partition for the data cloud (see methods), regression analysis found no significance for the upper region \((R^2 = 0.08; P = 0.223)\) nor for the lower region \((R^2 = 0.001; P = 0.907)\).

**Habitat Patterns**

Nearly seventy percent (69.6%) of introduced species (for which a habitat association was available) were associated with wasteland, urban, agricultural or disturbed habitats. In marked contrast, 65% of native species inhabit woodland or woodland habitats in combination with others, and a further quarter of native species were associated with wetlands. \(\chi^2\) contingency analysis revealed that exotic species were significantly over-represented in disturbed and wasteland habitats, and under-represented in woodland, woodland-thicket, open woodland, wetland, and woodland-woodland habitats (Table II). Exotic species were also significantly over-represented by species growing on moist substrates and under-represented by species preferring wet soils (Table II).

When all communities were considered together (from Table II), the Pearson’s coefficient of correlation was slightly negative \((r = -0.196, P = 0.642)\), suggesting a very slight relationship between decreasing numbers of exotic and increasing numbers of native taxa. However, when the community type called ‘disturbed-wasteland’ was excluded, the correlation coefficient was stronger and positive \((r = 0.607, P = 0.148)\). This suggests that exotics, excluding the suite that require disturbance, are slightly more likely to be found in more diverse communities.

**Table II. Results of \(\chi^2\) contingency analysis of the frequency of native and exotic species in various habitat types in southwestern Ontario (* = significantly over-represented; underline = significantly under-represented; \(P < 0.05\)).**

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Native</th>
<th>Exotic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open (meadow and prairie)</td>
<td>67</td>
<td>28</td>
</tr>
<tr>
<td>Woodland</td>
<td>392*</td>
<td>26</td>
</tr>
<tr>
<td>Woodland-thicket</td>
<td>63*</td>
<td>4</td>
</tr>
<tr>
<td>Open and woodland</td>
<td>170*</td>
<td>23</td>
</tr>
<tr>
<td>Wet</td>
<td>205*</td>
<td>23</td>
</tr>
<tr>
<td>Open and wet</td>
<td>49</td>
<td>2</td>
</tr>
<tr>
<td>Woodland and wet</td>
<td>68*</td>
<td>4</td>
</tr>
<tr>
<td>Disturbed-wasteland</td>
<td>52</td>
<td>256*</td>
</tr>
<tr>
<td>Overall (\chi^2) = 784.43; (P &lt; 0.001)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Soil moisture**

<table>
<thead>
<tr>
<th>Soil moisture</th>
<th>Native</th>
<th>Exotic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>254</td>
<td>34</td>
</tr>
<tr>
<td>Dry - moist</td>
<td>152</td>
<td>12</td>
</tr>
<tr>
<td>Moist</td>
<td>365</td>
<td>83*</td>
</tr>
<tr>
<td>Moist - wet</td>
<td>88</td>
<td>9</td>
</tr>
<tr>
<td>Wet</td>
<td>304</td>
<td>22</td>
</tr>
<tr>
<td>Overall (\chi^2) = 30.47; (P &lt; 0.001)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Life-History Patterns**

Exotic species generally favoured certain life history strategies, while broadly under-utilizing others (Table III). Exotics were significantly over-represented by the annual or biennial life cycles, hermaphroditism, longer flowering periods, and very small fruit sizes (Table III). They were under-represented by the perennial life cycle, monococism and dioecism, a flowering period of two months, animal seed dispersal, and relatively medium-sized fruits (5.1-10 mm; Table III). From May until November, the mean (± SD) proportion of exotic species in flower in any month (28.7% ± 22.6 of species in flower/month) was greater than for natives (21.5% ± 16.2 of species in flower/month) \((t = -2.795; P = 0.023)\).

Figure 4 summarizes schematically the hierarchy of major strategies that exotic and native species use when co-occurring. Native species are largely insect- and wind-pollinated perennials, occurring in both successional and stable communities, while exotic species are both annual and perennial, wind-pollinated species thriving in early successional communities (especially wasteland habitats).

**Exotic Species and Natural Communities**

Separate analyses of habitat association and life history features were carried out comparing native species with exotic species found in relatively undisturbed natural habitats. Exotic species were significantly over-represented in open (meadow and prairie) habitats and were associated with moist substrates; they were under-represented in woodland communities (Table IV). Exotic species were also over-represented by the tree growth habit, a longer flowering season, and many seeds per fruit (Table IV).

**Vegetative Reproduction**

Of 1043 native perennials, 44.7% (466) have clonal organs. 39.7% (99) of 249 exotic perennials also have clonal organs, and the difference (using \(\chi^2\) test) was not significant \((P > 0.05); see Table III). Similar proportions are observed for those species only inhabiting intact community types, where 37.3% of native perennials and 35.7% of exotic perennials have clonal organs. Similarly, 42.5% of exotic perennials which were associated with disturbed habitats have clonal organs.
TABLE III. Results of χ² contingency analysis of life history features of exotic and native species in southwestern Ontario (* = significantly over-represented; underline = significantly under-represented; \( P < 0.05 \)).

<table>
<thead>
<tr>
<th>Life cycle</th>
<th>Annual and biennial</th>
<th>Perennial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>167</td>
<td>1043*</td>
</tr>
<tr>
<td>Exotic</td>
<td>203*</td>
<td>249</td>
</tr>
<tr>
<td>Overall χ²</td>
<td>182.22; ( P &lt; 0.001 )</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Growth habit</th>
<th>Herb</th>
<th>Shrub</th>
<th>Tree</th>
<th>Liana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>1085</td>
<td>144</td>
<td>67</td>
<td>14</td>
</tr>
<tr>
<td>Exotic</td>
<td>407</td>
<td>38</td>
<td>26</td>
<td>8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Clonal</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Exotic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Expected</td>
<td>99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( χ² = 1.55 ) ns</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Sex habit</th>
<th>Andromonoecious</th>
<th>Dioecious</th>
<th>Sex habit</th>
<th>Gyno-monoecious</th>
<th>Monoecious</th>
<th>Hermaphrodite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>18</td>
<td>74</td>
<td>73</td>
<td>224*</td>
<td>914</td>
<td></td>
</tr>
<tr>
<td>Exotic</td>
<td>4</td>
<td>12</td>
<td>32</td>
<td>20</td>
<td>385*</td>
<td></td>
</tr>
<tr>
<td>Overall χ²</td>
<td>30.19; ( P &lt; 0.001 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Pollination</th>
<th>Insect</th>
<th>Wind</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>121</td>
<td>375</td>
</tr>
<tr>
<td>Exotic</td>
<td>28</td>
<td>119</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Maximum length of flowering season (months)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
</tr>
<tr>
<td>Native</td>
</tr>
<tr>
<td>Exotic</td>
</tr>
<tr>
<td>Overall χ²</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Seed dispersal</th>
<th>Animal</th>
<th>Wind</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>102</td>
<td>426</td>
</tr>
<tr>
<td>Exotic</td>
<td>16</td>
<td>139</td>
</tr>
<tr>
<td>Overall χ²</td>
<td>6.17; ( P &lt; 0.05 )</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fruit size</th>
<th>0.1-5</th>
<th>5.1-10</th>
<th>10.1-20</th>
<th>20.1-50</th>
<th>&gt; 50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
<td>311</td>
<td>174*</td>
<td>69</td>
<td>54</td>
<td>28</td>
</tr>
<tr>
<td>Exotic</td>
<td>217*</td>
<td>49</td>
<td>26</td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td>Overall χ²</td>
<td>28.16; ( P &lt; 0.001 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Seeds per fruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native</td>
</tr>
<tr>
<td>Exotic</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

\(^{a}\) Expected value derived from the proportion of native perennials that are clonal.

Common, rare, and introduced plant species

Terrestrial

Habitat

Low human disturbance

Successional

Wasteland

Wetland

Life cycle

Annual

Perennial

Pollination

Insect

Wind

Habitat

Life cycle

Annual

Perennial

Pollination

Insect

Wind

Native

1 2 21 32 0 1 10 14 0 1 0 0 0 2 2 18

Introduced

0 0 9 9 1 11 5 18 1 29 2 11 0 1 1 1

**FIGURE 4.** Dendrogram showing the percentages of native and introduced species with different habitat, life cycle and pollination strategies in southern Ontario plants.
TABLE IV. Summary of the re-analysis of exotic-native differences using only exotic species that inhabit less disturbed and natural communities. Traits that proved significant (*P < 0.005), using χ² contingency analysis, are shown (∗ = significantly over-represented; underline = significantly under-represented; *P < 0.05).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Native species</th>
<th>Exotic species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open (meadow and prairie)</td>
<td>67</td>
<td>28*</td>
</tr>
<tr>
<td>Woodland</td>
<td>392</td>
<td>26</td>
</tr>
<tr>
<td>Woodland-thicket</td>
<td>63</td>
<td>4</td>
</tr>
<tr>
<td>Open and woodland</td>
<td>170</td>
<td>25</td>
</tr>
<tr>
<td>Wet</td>
<td>205</td>
<td>23</td>
</tr>
<tr>
<td>Open and wet</td>
<td>49</td>
<td>2</td>
</tr>
<tr>
<td>Woodland and wet</td>
<td>68</td>
<td>4</td>
</tr>
<tr>
<td>Overall χ² = 53.53; P &lt; 0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Soil Moisture</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>254</td>
<td>18</td>
</tr>
<tr>
<td>Dry - moist</td>
<td>152</td>
<td>5</td>
</tr>
<tr>
<td>Moist</td>
<td>365</td>
<td>45*</td>
</tr>
<tr>
<td>Moist - wet</td>
<td>88</td>
<td>4</td>
</tr>
<tr>
<td>Wet</td>
<td>304</td>
<td>18</td>
</tr>
<tr>
<td>Overall χ² = 15.07; P &lt; 0.005</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Growth habit</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Herb</td>
<td>1085</td>
<td>85</td>
</tr>
<tr>
<td>Shrub or small tree</td>
<td>144</td>
<td>14</td>
</tr>
<tr>
<td>Tree</td>
<td>67</td>
<td>20*</td>
</tr>
<tr>
<td>Liana</td>
<td>14</td>
<td>2</td>
</tr>
<tr>
<td>Overall χ² = 26.23; P &lt; 0.001</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Maximum length of flowering season (months)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>58</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td>392</td>
<td>35</td>
</tr>
<tr>
<td>3</td>
<td>309</td>
<td>21</td>
</tr>
<tr>
<td>4</td>
<td>169</td>
<td>27</td>
</tr>
<tr>
<td>5</td>
<td>22</td>
<td>6*</td>
</tr>
<tr>
<td>6 or more</td>
<td>7</td>
<td>4*</td>
</tr>
<tr>
<td>Overall χ² = 24.19; P &lt; 0.001</td>
<td></td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Seeds per fruit</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Single</td>
<td>646</td>
<td>47</td>
</tr>
<tr>
<td>Few (2-3)</td>
<td>170</td>
<td>26</td>
</tr>
<tr>
<td>Several (4-6)</td>
<td>104</td>
<td>7</td>
</tr>
<tr>
<td>Many (&gt; 7)</td>
<td>243</td>
<td>36*</td>
</tr>
<tr>
<td>Overall χ² = 14.57; P &lt; 0.005</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Clonal\(^a\)               | 41.80 (expected) | 40             |
| χ² = 0.08 ns                | 0.8          |

\(^a\) Expected value derived from the proportion of native perennials that are clonal.

TAXONOMIC REPRESENTATION

Weber (1997) found that global family size was a strong predictor of the number of exotic species per family in Europe (R² = 0.74; *P < 0.001). Global family size also predicts the number of exotic species in southwestern Ontario, although this relationship does not explain as much of the variation (R² = 0.35). Other factors are evidently also important, suggesting that species not native to southwestern Ontario are not simply a random sample from a larger pool of species. Analysis showed that certain families were much more likely than others to be represented by exotic species. This further supports the idea that other factors contribute to the success of exotic species.

PERSISTENCE IN A DEGRADED LANDSCAPE

-The condition of overwhelming importance for exotic species establishing themselves is large-scale anthropogenic disturbance and alteration of formerly natural habitats (Baker, 1974; Crawley, 1986; Rejmánek, 1989; Pysek, Prach & Smilauer, 1995; Lonsdale, 1999). In an elegant experiment, Burke and Grime (1996) showed that the susceptibility of a native community to invasion was strongly related to the level of disturbance (especially when disturbance coincided with eutrophication). In southwestern Ontario, exotic species appear to be generally very poor invaders of undisturbed habitats. The smaller number of introduced species found in habitats such as intact woodland, wetland, and woodland/prairie suggests that these communities are less invisible, in contrast to intensively or regularly-disturbed habitats, which create environments with low local competition (Crawley, 1986; Kotanen, 1997). Native species richness itself is unlikely to be the factor for deterring the invasion of exotics (Lonsdale, 1999; Levine, 2000). Individual species that are successful in natural communities, such as Lythrum salicaria, for example, can do significantly more harm to biodiversity by proliferating in natural wetlands than the many species that invade disturbed and arable land. Interestingly, Rejmánek (1989) found that mesic communities are more invisible than dry or aquatic communities. Exotic species in our study region appear to confirm this observation.

Given (1994) summarized the array of characteristics facilitating persistence in exotic plants. Some species persist locally within urban areas where there are particular conditions allowing them to survive (e.g., moisture, warmth). These species tend to have little impact on native vegetation. Second, some flourish in heavily disturbed habitats (e.g., wasteland, roadsides, landfills). These can compete with native fugitive species. For example, in southern Ontario, yellow rocket (Barbara vulgaris) is closely associated with disturbed fields and an agricultural landscape (MacDonald & Cavers, 1991). Furthermore, disturbance usually facilitates invasion. Populations of exotics (especially exotic annuals) often recover from disturbance faster than those of natives (Kotanen, 1997). An example is Queen Anne's lace (Daucus carota carota) invading tallgrass prairie habitat (Parker, Mertens & Schemske, 1993). Third, some species invade native habitat and can displace native species, especially in dunes, grassland, and wetland. Examples include glossy buckthorn (Rhamnus frangula), which is spreading across southern Ontario from the urban centers where it was intro-

Discussion

Although the proportion of exotics in the southwestern Ontario flora (26%) is not as great as in some other floras, (e.g., 46% in the British Isles), they still constitute a significant fraction. Degradation of the southern Ontario landscape over the past 300 years is surely not as extensive and sustained as in Britain over the past 3000 years, despite the fact that some Ontario townships have up to 99% of the landscape disturbed (Maycock & Fahselt, 1987).

These analyses were based on a series of testable hypotheses. First, we tested whether particular taxonomic families were disproportionately represented by exotic species; and second, whether exotic species rely disproportionately (compared to natives) on the availability of disturbed habitat. Another seven hypotheses, given by Baker (1986), are outlined in the Introduction and discussed here.
duced (Catling & Porebski, 1994) and purple loosestrife (Lythrum salicaria) which has had a major impact on wetland vegetation in southern Ontario (Mal et al., 1992; Mal & Lovett-Doust, 1997). In wetland habitats in particular, rare species tend to be affected more than common species, because of their lower abundance (Weiher & Keddy, 1995).

Southern Ontario, being largely agricultural, has many annually disturbed habitats making them inhospitable to slow-growing, long-lived species. In their comparative study of the British flora, Crawley, Harvey and Purvis (1996) found that the frequency of introduced and native species did not differ in terms of their life cycle. We observed that exotics were significantly over-represented by the annual and biennial life cycles, compared to common species. It appears as though short-lived, rapidly reproducing invaders thrive in this landscape.

CLIMATE AND PLACE OF ORIGIN

Baker’s (1986) first characterization of exotic species is that they probably come from regions having similar climates. The overwhelming majority of alien species found in Europe originate from North America and Asia (Pysk, Prach & Smilauer, 1995; Weber, 1997), while in southern Ontario the opposite is true: exotic plants come mostly from Europe and Asia. Economic globalization and international transport has fostered a reciprocal exchange of species among north-temperate regions. Fewer than ten percent of southern Ontario exotics come from elsewhere on the North American continent. These species would presumably be phylogenetically closer to species that are adapted to existence in our region, but perhaps the abundance of European and Asian taxa reflects the capacity of species coming from similar climatic regimes to prosper over species from different (but geographically closer) climates (Baker, 1986).

SIMILAR LIFE FORMS

Baker’s second suggestion, that invaders and natives ought to have similar life forms, appears to be supported by our results, with one minor exception. When comparing natives and exotics which only occur in relatively undisturbed communities, southern Ontario exotics were significantly over-represented by trees. Many of these species (such as Acer spp., Populus spp., Prunus spp., and Ulmus spp.) have been selectively introduced by humans, for ground cover, soil improvement, erosion control, wind breaks, and horticulture (Catling, 1996).

SIMILAR SOIL TYPES

Exotic species were over-represented among moist soils, but it would be incorrect to assume this represents their preferred soil moisture in their place of origin. More data, including soil composition and soil conditions of invading species in their native range are required to test this hypothesis.

GENERALIZED POLLINATION SYSTEM

Our results did not reveal any differences with respect to pollination syndrome. Of course, this does not disprove Baker’s hypothesis. Temperate species predominantly have generalized pollination syndromes compared to, say, tropical species (for example, Ficus spp., see Nason & Hamrick, 1997). We would expect species invading temperate communities, where most species rely on wind dispersal, not to have significantly different proportions of individuals with differing pollination syndromes.

ABILITY TO DISPERSE SEEDS

Baker’s thesis here is simple: invasive species will need to utilize the simplest and most effective mode of dispersal to get to and move within a new habitat. Our results show that exotics are under-represented by animal dispersal. Reduced reliance on animal vectors, which may or may not occur in new habitats, would probably bode well for exotics. However, wind-dispersal may not be the vector explaining why some invasive taxa appear to be able to traverse great distances in establishing new populations (Cain, Milligan & Strand, 2000), though human activity (e.g., transportation systems) may be an important vector. We need to understand the long-distance dispersal ability of plants, especially in an altered landscape, if we are to produce accurate predictions of invasions (Cain, Milligan & Strand, 2000).

REPRODUCTIVE STRATEGY

Baker’s (1986) logic dictates that invasive species ought to be able to successfully reproduce in low numbers, while maintaining genetic diversity. Our results show that exotics are over-represented by the hermaphroditic sex habit, which would facilitate Baker’s reproductive requirements. Ignoring genetic and biochemical self-incompatibility (for which there are no flora-wide data), hermaphroditism could allow for self-fertilization, or pollination among closely related individuals, while maintaining genetic variation through recombination (Silvertown & Lovett-Doust, 1993). In an early experiment, Mulligan & Findlay (1970) showed that 100% of 33 invasive annuals and 21 of 23 biennials set viable seed with self-fertilization.

VEGETATIVE INVASIONS

Baker (1974; 1986) concluded that clonal species ought to make better invaders, but our results do not support this. More recently, Pysk (1997b) showed that clonality is context-dependent as an invasive trait. In his analysis of the Central European flora, Pysk showed that clonality was more important in wetter, colder regions and less so in warmer, drier areas. Pysk (1997b) also showed that clonality was more useful in invading natural communities and less so in disturbed ones. In considering exotics that only occur in natural communities, we did not find exotics to be significantly over-represented by the presence of clonal organs. Furthermore, we found that exotic perennials inhabiting disturbed communities were equally likely to have a clonal organ. It appears as though perennials in general (native, exotic, and those associated with both intact and disturbed communities) have a high incidence of clonal growth, making this attribute a poor indicator of invasibility for this region. Rather, these exotics tended toward longer flowering seasons and the production of many-seeded fruits, as possible competitive advantages for spreading into new areas.

Finally, although we have found trends that aid in explaining generalized differences between native and common species, it is clear that no single trait or group of
attributes can consistently describe all weeds (see too Williamson & Fitter, 1996). Furthermore, examining the suite of hypotheses, the only one the present data do not support was Baker's (1986) assertion that vegetative reproduction would assist species in the invasion of intact communities. The other eight hypotheses appear to describe legitimate mechanisms by which exotic species colonize and expand their range, in this case into southwestern Ontario. The presence of exotic species here appears to be a product of a number of phylogenetic and life history factors; nevertheless, the majority of these exotics thrive because of particular features supporting success in fragmented and disturbed landscapes.

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Literature cited


