

Evolutionary and ecological influences of plant invader success in the flora of Ontario¹

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Abstract: It is not clear why some species are able to naturalize and spread in a new region while so many other species are not. Several general properties have been reported for successful non-indigenous plant species (NIPS). These include presence of a lag time and population expansion following invasion, arrival from a similar climate, ability to self-fertilize, a short lifespan, clonal growth (if perennial), and production of small fruits. We examined these patterns in comparisons of all recorded abundant and rare NIPS in Ontario ($n = 1153$). We used cross-species and phylogenetic regressions to examine ecological patterns across present-day species and to determine whether evolutionary divergences in NIPS success have been correlated consistently with divergences in any of the life-history traits. We found a significant time lag in invader spread, with species arriving after 1952 being more likely to be rare. Successful invaders (*i.e.*, abundant NIPS) were significantly over-represented among species originating in Europe and Eurasia. Successful invaders were significantly more likely to demonstrate clonal growth, to grow on variable soil moistures, and to have comparatively long flowering periods. While analyses such as this do not reveal causal mechanisms for the observed patterns, our correlative findings suggest important mechanisms for NIPS success that we discuss in light of the theoretical expectations of the attributes of successful plant invaders.

Keywords: database analysis, ecological generalities, exotic success, life history attributes of invaders, naturalization, phylogenetic regression.

Résumé : Il n'est pas évident pourquoi certaines espèces sont capables de se naturaliser et de se propager avec succès dans une nouvelle région alors que plusieurs autres ne le sont pas. De nombreuses propriétés générales des plantes non indigènes (NIPS : Non indigenous plant species) ayant du succès ont été rapportées. Celles-ci incluent la présence d'un décalage et l'expansion de la population après l'invasion, la provenance d'un climat similaire, ainsi que la capacité de s'auto-fertiliser, une courte durée de vie, la croissance végétative (dans le cas de plantes pérennes) et la production de petits fruits. Nous avons examiné ces patrons pour toutes les NIPS abondantes et rares observées en Ontario ($n = 1153$). Nous avons utilisé des régressions sur plusieurs espèces et sur leur phylogénétique pour examiner les patrons écologiques des espèces présentes aujourd'hui et déterminer si des divergences évolutives dans le succès des NIPS sont corrélées de façon régulière avec des divergences dans les traits d'histoire de vie. Nous avons trouvé un décalage significatif dans la propagation des espèces envahissantes, celles arrivées après 1952 ayant plus de chance d'être rares. Les envahisseurs ayant eu du succès (*i.e.*, NIPS abondantes) étaient significativement surreprésentés parmi les espèces originaires d'Europe et d'Eurasie. En comparaison, un plus grand nombre de ces envahisseurs démontrait de la croissance végétative et une capacité à croître sur des sols ayant différents taux d'humidité tout en possédant des périodes de floraisons significativement plus longues. Même si de telles analyses ne révèlent pas les mécanismes responsables des patrons observés, nos résultats de corrélation suggèrent d'importants facteurs contribuant au succès des NIPS dont nous discutons à la lumière des prévisions théoriques au niveau des attributs des plantes envahissantes.

Mots-clés : analyse de base de données, généralités écologiques, naturalisation, régression phylogénétique, succès d'exotiques, traits d'histoire de vie d'envahisseurs.

Introduction

Historical boundaries on species distributions have been imposed by both physical and biological limits. However, with the advent of unlimited global human dispersal over the past 500 y, Earth's biota is undergoing a breakdown of those historical barriers and a concomitant mass spread of species to new regions (Drake *et al.*, 1989; Mack *et al.*, 2000; Lockwood & McKinney, 2001). All this is occurring at a geologically unprecedented scale (Vermeij, 1991).

Given the existence of homogenizing forces acting upon the biota, ecologists are faced with the task of trying to understand the abundance patterns of particular non-indigenous species (NIS).

For over 40 y, ecologists have been trying to develop generalities associated with non-indigenous plant species (NIPS) success. Famously, Herbert Baker listed the traits of an ideal weed (Baker, 1965; 1986). Of course, he was explicitly addressing weedy species in disturbed habitats, but more recently others have also attempted to develop general rules of plant invasiveness (Rejmanek, 1996). With the advent and accessibility of large electronic species lists, ecologists have begun to test for generalities in plant inva-

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sions (Cadotte, Murray & Lovett-Doust, 2006). Since the early 1990s several studies have examined the distribution of plant traits across large databases in an attempt to understand patterns of plant invasions (Crawley, Harvey & Purvis, 1996; Williamson & Fitter, 1996; Daehler, 1998; Pyšek, 1998; Cadotte & Lovett-Doust, 2001; Pyšek *et al.*, 2003). In a review of NIS studies, Kolar and Lodge (2001) determined that several general life history and ecological properties were associated with NIPS success. These included a previous history of invasion success, a close phylogenetic relationship with successful invaders, clonal growth, constant seed crop size, and reduced juvenile period. The first two patterns rely on a previous history of invasions and are not as useful in predicting the mechanisms underpinning successful invasions (who makes a good invader? Invaders do). It is important to note that the studies reviewed by Kolar and Lodge (2001) greatly varied in sample size and type of species list. We have argued (Cadotte, Murray & Lovett-Doust, 2006) that large species databases that attempt to enumerate all or most species in a region may be the best way to test for generalities of NIS.

Since the Kolar and Lodge (2001) review, several studies have examined large (*e.g.*, > 600 species) datasets (Cadotte & Lovett-Doust, 2001; Thébaud & Simberloff, 2001; Pyšek *et al.*, 2003). These studies use whole invasive floras of NIPS to address general questions in invasion biology. A major focus of invasion biology involves how and why some species, upon entering a new region, spread and achieve high population abundances (*i.e.*, they become naturalized or invasive), while in contrast many other species are simply present, either never becoming abundant or failing completely to thrive and possibly dying out in the introduced region.

Plant naturalization likely happens for many reasons. Indeed, the processes leading to persistent rarity or abundance in introduced species may be multifaceted and can be examined on a number of levels (*e.g.*, population processes, community attributes and dynamics, and broad biogeographical and phylogenetic patterns and processes). A key goal of invasion biology is to find robust generalities correlated with invader success. In this paper we examine life history generalities that distinguish successful NIPS from other NIPS.

Here we use a database of all recorded non-indigenous angiosperm taxa ($n = 1153$) found in Ontario, Canada. Ontario's biological diversity is concentrated in the southern third of the province, so the NIPS used in this analysis are concentrated in the south as well. Ontario's first wave of human colonization occurred about 12,000 y before present, after human populations crossed the Bering Strait from Asia and spread across the Americas. A second wave, consisting of European immigrants, started about 300 y ago and continues today with immigrants from all over the world. As a result of the plants that travelled with these colonization waves, more than one quarter of Ontario's flora are NIPS (Cadotte & Lovett-Doust, 2001). We examine the influences of geographic origin, relative time of introduction, sex habit, life cycle, fruit size, flowering duration, clonality, and soil associations on the abundance of the NIPS in Ontario. We expect that geographic origin will be important, specifically,

that species from similar climates (in Europe and Asia) will be more likely to be successful in Ontario (Baker, 1986; Williamson & Fitter, 1996; Cadotte & Lovett-Doust, 2001; Prinzing *et al.*, 2002). We expect also that there is a time lag present, and that the longer a species is present in a new territory the higher the probability it may become abundant (Scott & Panetta, 1993; Mack *et al.*, 2000; Pyšek *et al.*, 2003). We expect that successful NIPS will have a suite of life history attributes, for example being self-fertilizing (including no herkogamy), having an annual or short-lived life-cycle, producing small, easily dispersed fruits or seeds, and having earlier and longer flowering periods (Baker, 1986; Anderson, 1995; Daehler, 1998; Cadotte & Lovett-Doust, 2001; but *cf.* Crawley, Harvey & Purvis, 1996).

Methods

The set of 1153 non-native angiosperm taxa (hereafter referred to as non-indigenous plant species, or NIPS) used in this analysis came from the Ontario Ministry of Natural Resources, Natural Heritage Information Centre (NHIC, 2005). The NHIC database includes estimates of abundance using a provincial ranking system (S-rank) as follows:

- SE1: Non-native species is extremely rare; five or fewer occurrences.
- SE2: Non-native species is imperilled; between six and twenty occurrences.
- SE3: Non-native species is rare to uncommon; between 21 and 100 occurrences.
- SE4: Non-native species is common; > 100 occurrences.
- SE5: Non-native species is demonstrably widespread and secure.

We excluded from our analysis all species that had uncertain or historical abundance status ($n = 301$) to avoid miscalculation of NIPS success. Large-scale abundances, such as those used here, may be a more efficacious scale than smaller scales in determining the ecological and evolutionary factors driving invasions since specific local, historical, and environmental vagaries are minimized (Hamilton *et al.*, 2005).

We categorized species into three time-of-arrival groups. The first group consisted of species present in Ontario prior to 1952, which were listed as being present in eastern North America by Gleason (1952). The second group consisted of species that arrived in Ontario between 1952 and 1979 and thus were not listed in Gleason (1952) but were listed in Scoggan (1979). The final group were listed in neither Gleason nor Scoggan but were listed as present by the NHIC; these were considered to have arrived after 1979.

Region of origin was ascertained for the large group of NIPS present in Ontario before 1952 (representing *ca* 74% of exotics) from Gleason (1952). We analyzed the influence of various life history attributes on the relative abundance of plants in this group. We used only pre-1952 species to control for the effect of time of introduction, since species introduced more recently have a lower probability of being widespread. Life history traits, obtained from Gleason (1952), included four continuous variables: flowering duration (months), number of seeds per fruit, relative fruit

size, and typical height; and seven categorical variables: sex habit, life cycle, flowering period, presence of a clonal organ, life form, soil moisture preferences, and geographic origin (see Table I for categories for each categorical variable).

ANALYSES

When undertaking species comparisons in large data sets, one must be cognizant of underlying assumptions involved in species analyses (Cadotte, Murray & Lovett-Doust, 2006). Analyzing species patterns as individual data points (cross-species analysis) simply models the relationship between ecological variables and species abundances. However, as Felsenstein (1985) argued, species and their life history attributes share evolutionary history, and this may influence interpretation of life history relationships across numerous species. Felsenstein (1985) advocated incorporating phylogenetic information into multi-species analyses. There is not universal agreement on interpreting phylogenetically informed analyses (Westoby, Leishman & Lord, 1995), however, so we used both cross-species and phylogenetically informed analyses to discern the relationship between life history attributes and NIPS abundance. For cross-species analyses, we used generalized linear models in SAS (version 9.2), modeling NIPS abundance as the dependent variable and the various life history attributes as independent variables.

We also employed phylogenetic regressions (Grafen, 1989) to carry out correlated divergence analysis. Here, phylogenetic information for the study species was incorporated in regression analyses to determine whether evolutionary divergences in abundances correlate consistently with divergences in any of the life history traits. Phylogenetic regressions were performed using a generalized linear interactive modeling program (Phylo.glm version 1.03; Grafen, 1989). Abundance was modeled as the dependent variable, with life history traits as independent variables. The database of trait values for extant species was transformed in a process referred to as "hanging on a tree" (Grafen, 1989). This procedure is based on the "radiation principle" (Ridley, 1983; Grafen, 1989), under which each radiation in the phylogeny—rather than each species—constitutes an independent data point (Felsenstein, 1985; Harvey & Pagel, 1991). Data points at each radiation are calculated as averages based on the values of daughter nodes in the phylogeny (averages are

weighted according to the path segment length). The question asked is whether a change in abundance is related to a change in the life history variables along the same phylogenetic branch.

Construction of a working phylogeny was required for phylogenetic regression analyses. This process was automated by the Phylomatic database (Chazdon *et al.*, 2003). Details on the full assembly rules and source information for the phylogeny are available at the Phylomatic website (Webb & Donoghue, 2002). Phylomatic constructs a phylogenetic tree based on a phylogenetic "mega-tree" assembled from global data sets. Path segment lengths for the phylogeny were calculated in phylogenetic regressions by assigning a height to each node that was one less than the number of species below or at that node in the tree (Grafen, 1989).

First we analyzed separately each independent variable in its own model. To control for intercorrelations among independent variables, we then performed a second analysis, which determined the unique contribution of each independent variable in explaining NIPS abundance. Here separate analyses were carried out for each independent variable, within which all independent variables other than the test variable were entered as control variables. This was done for both the cross-species and the phylogenetic regressions

Results

There were 1153 recorded NIPS in Ontario. The majority of these exotic species were relatively rare (SE1, SE2, and SE3: 65.9%), hermaphroditic (85.1%), perennial (53.7%), late-season bloomers (73.8% had a flowering season that extended past August), herbaceous (86.7%), and of European or Eurasian origin (64.6%) (see Appendix I). Several life history attributes appeared to have non-random distributions with respect to NIPS abundance (Appendix I).

Of the 1153 NIPS, 846 were introduced prior to 1952, 183 between 1952 and 1979, and 124 after 1979. Species that arrived after 1952 were significantly more likely to be rare (SE1 abundance status) and less likely to be common (SE5 status) compared to pre-1952 arrivals (Figure 1). For this confounding reason, all species that arrived after 1952 were excluded from the life history analysis. These species were considered less likely to have reached equilibrium abundances.

LIFE HISTORY ANALYSIS

When each trait was modeled separately with NIPS abundance (Table II), the presence of a clonal organ, increased flowering duration, and flowering throughout the growing season were features that distinguished common from rare NIPS. In relation to preferred soil type, common NIPS were found to grow in variable soil moistures rather than being specialized on a particular soil moisture. The geographic origin of species also played a significant role in distinguishing rare from common NIPS. NIPS from Asia, Africa, the Mediterranean, Tropical America, and North America were significantly less likely to be common. In contrast, species from Europe and Eurasia were more likely to be common. Divergences in fruit size, height, life cycle, life form, and seeds per fruit were not related to divergences

TABLE I. The seven categorical variables used in this analysis.

Life history trait	Number of levels	Categories recorded
Clonal organ	2	Present or absent
Flowering season	4	Early, mid, late, and all season
Geographic origin	7	Asia, Eurasia, Europe, Mediterranean, North America, Tropical America, and Africa
Life cycle	3	Annual (& biennial), perennial, and variable
Life form	4	Herb, shrub, tree, and vine
Sex habit	4	Monoecious, dioecious, hermaphrodite, and polygynous
Soil moisture	6	Dry, moist-dry, moist, moist-wet, wet, and variable

in abundance (Figure 2). These results were robust regardless of whether phylogenetic information was used or not (Table II).

In analyses that attempted to control for the influence of the other life history traits, flowering duration, geographic range, and soil type continued to predict NIPS abundance (Table III). Moreover, after controlling for the influence of all other life history traits in the model for sex habit, it emerged that polygynous species (those having many pistils or styles) were more likely to be abundant compared with monoecious, dioecious, or hermaphroditic species (Table III). However, so few species were listed by Gleason (1952) as polygynous (as opposed to a specific sex habit; $n = 3$) that this result will not be discussed.

Discussion

In a previous paper (Cadotte, Murray & Lovett-Doust, 2006), we argued that database analyses may be the best way to uncover ecological generalities, because such studies are less susceptible to several potential problems, including biases of species selections, as well as those due to the vagaries of time and space. Moreover, such studies can readily be blended with other database analyses. Ecological systems are arguably the most complicated systems in nature, and predicting which species will have what impact may not be possible (Williamson, 1999) due to the complex nature of species interactions with other species and their environments. This complexity is apparent in the multitude of diverse hypotheses created to explain plant invasiveness (see Inderjit, Cadotte & Colautti, 2005). We posit that with generalities we can identify high-risk species and offer potentially fruitful avenues of research to uncover mecha-

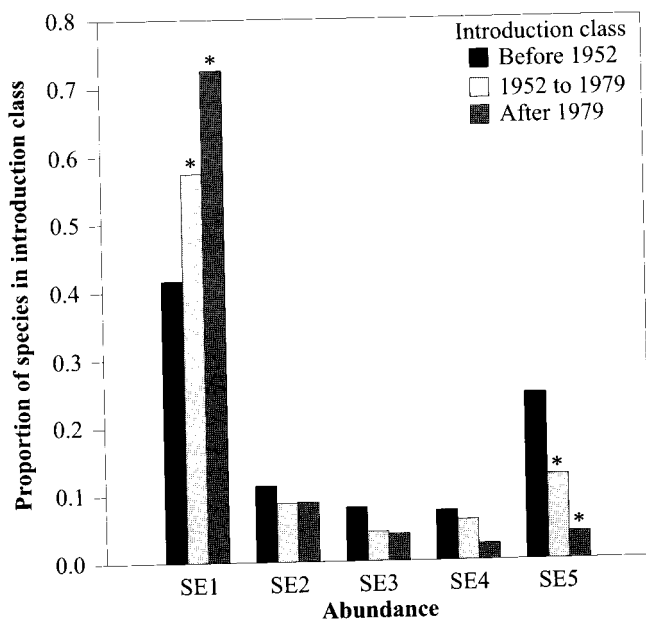


FIGURE 1. The proportion of species in the three time-of-introduction classes for each abundance class, where SE1 is the rarest and SE5 the most abundant. Asterisks indicate the results of chi-square analysis comparing relative abundances in the two latter introduction classes to those in the pre-1952 introduction class. * = $P < 0.0005$ (Bonferroni corrected, α/k).

TABLE II. Results of cross-species and phylogenetically informed analyses modeling abundance as the dependent variable and each life history trait as a separate independent variable. Predictor variables with $P < 0.1$ are in bold.

Trait	Cross-species			Phylogenetically-informed		
	F	df	P	F	df	P
Clonal organ	6.64	1, 647	0.010	4.94	1, 186	0.03
Flowering duration	10.85	1, 454	0.0011	11.38	1, 140	0.001
Flowering season	2.29	3, 457	0.034	5.92	3, 138	0.0008
Fruit size	5.17	1, 514	0.023	4.04	1, 155	0.05
Geographic origin	8.46	6, 602	< 0.0001	9.27	6, 172	< 0.0001
Height	0.33	1, 591	0.57	0.26	1, 168	0.61
Life cycle	0.90	2, 627	0.41	0.29	2, 179	0.75
Life form	1.25	4, 638	0.29	0.49	4, 180	0.74
Seeds per fruit	0.74	1, 623	0.39	0.64	1, 180	0.42
Sex habit	1.21	5, 179	0.30	2.42	5, 179	0.04
Soil moisture	7.85	5, 281	< 0.0001	8.71	5, 105	< 0.0001

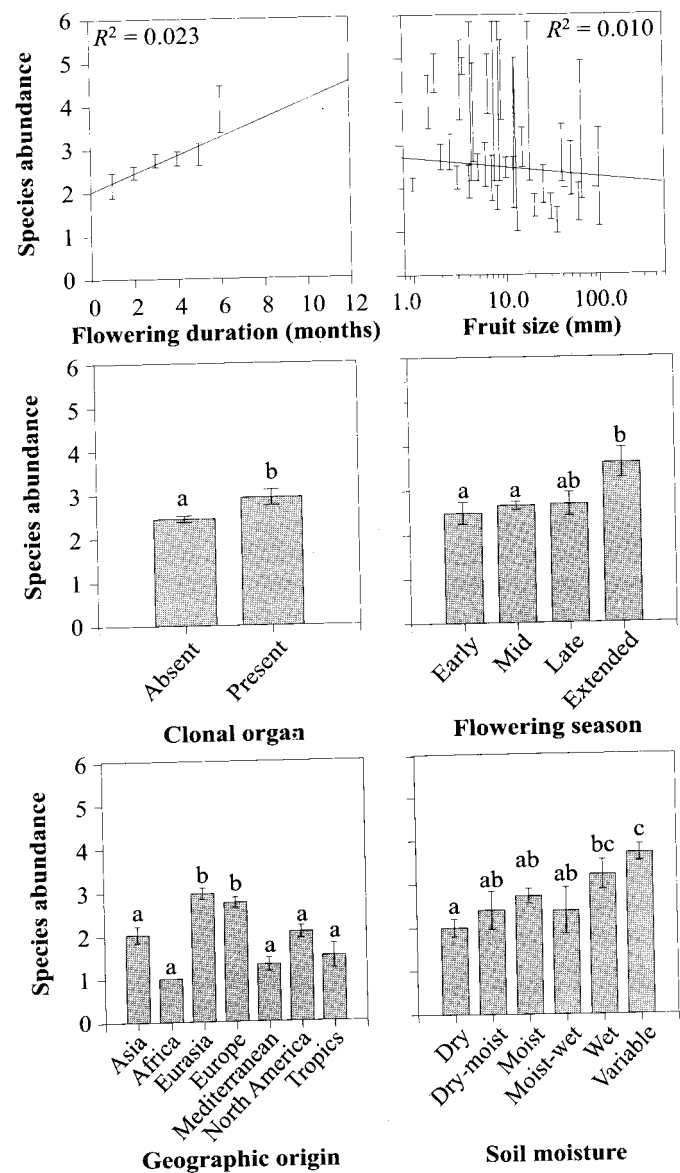


FIGURE 2. Variables significantly affecting non-indigenous species abundance. Different letters refer to significant differences ($P < 0.05$) from the univariate tests for the categorical variables.

TABLE III. Results of cross-species and phylogenetically informed analyses modeling abundance as the dependent variable with each life history trait after controlling for the influence of all other independent variables. Predictor variables with $P < 0.1$ are in bold.

Trait	Cross-species			Phylogenetically-informed		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Clonal organ	0.40	1, 149	0.53	0.36	1, 51	0.55
Flowering duration	3.51	1, 149	0.06	4.15	1, 51	0.05
Flowering season	0.60	3, 149	0.61	1.43	1, 51	0.24
Fruit size	1.86	1, 149	0.18	3.20	1, 51	0.08
Geographic origin	3.21	6, 149	0.009	6.65	5, 50	< 0.0001
Height	0.01	1, 149	0.94	0.28	1, 51	0.60
Life cycle	0.84	2, 149	0.43	2.12	1, 51	0.15
Life form	0.58	4, 149	0.68	1.61	4, 51	0.19
Seeds per fruit	0.08	1, 149	0.82	0.08	1, 51	0.78
Sex habit	0.31	5, 149	0.91	2.95	5, 50	0.02
Soil moisture	7.23	5, 145	0.008	2.08	5, 51	0.08

nisms of invasions. The present study is an example of an approach towards uncovering those general patterns.

It is important to point out that this study does not break invasions down into specific habitat types. Authors have found that plants entering different habitats may possess different sets of traits (Pyšek, 1997; Cadotte & Lovett-Doust, 2001). What our study does is try to find extremely broad-scale patterns and the factors correlated with these patterns.

In this study, we found several patterns associated with NIPS abundance in the Ontario flora. We showed that species arriving after 1952 were much more likely to be rare, and less likely to reach high abundances, than species arriving before 1952 (with many likely to have arrived many years before 1952). Pyšek and collaborators (2003) were able to find relative times of introduction for 50% of the introduced flora of the Czech Republic (668 of 1364 NIPS). That study had a much more fine-scale delineation of time of arrival, from a greater number of sources, spanning a longer period (six floras from 1809 to 1904, plus searches of the primary literature). Pyšek *et al.* (2003) found a much stronger negative relationship between abundance and year-of-arrival. Similarly, Castro and colleagues (2005) found that species with shorter residence times in Chile had smaller range sizes. It appears as though this is a widespread phenomenon (Scott & Panetta, 1993; Mack *et al.*, 2000; Kolar & Lodge, 2001). Possible reasons for this time lag are four-fold (Mack *et al.*, 2000). The first is scale of observation: small initial populations may indeed be rapidly growing, but we are often simply unable to observe this. Second, population isolation may appear as slow growth, but if there are several initial inoculations, overall growth will appear to be faster. Third, there may be a period of natural selection in the population, and the increase in population size or number could coincide with the appearance of an adaptive genotype. Finally, the transition of slow-to-fast growing populations may coincide with certain advantageous environmental cues or events.

In order to understand how the other factors (clonal organ, flowering duration, flowering season, fruit size, geographic origin, plant height, life cycle, life form, number of seeds, sex habit, and soil type) interact with the distribution of NIPS abundance we employed phylogenetically informed analyses. The two types of models we employed,

one with each variable treated independently and the other with all variables included as part of the model (Tables II and III, respectively), revealed slightly different results. The model that included all variables was more conservative, but depended on the number of variables incorporated and the completeness of the data. Different studies use different numbers of variables, ranging from a single trait (Pyšek, 1997; Thébaud & Simberloff, 2001) to 10 or more traits (Pyšek, Prach & Šmilauer, 1995; Thompson, Hodgson & Rich, 1995; Williamson & Fitter, 1996). Examining individual variables allows us to identify potentially important traits associated with invasiveness and enable comparison with other studies.

Our results suggest that parameters of reproduction (both vegetative and sexual) are important to NIPS success. This is not surprising, since we were essentially measuring population spread and abundance, and how these populations spread should be very important to their success. We found that small fruits were also correlated with NIPS abundance.

Our analysis showed that abundant NIPS were more likely to have a clonal organ. This is a feature that Baker (1965; 1986) predicted as being important for weedy species. Later, Pyšek (1997) showed that even though clonal species appear to be at a disadvantage during the dispersal phase of invasion, they were over-represented in less disturbed communities, possibly due to a greater competitive ability (Pyšek, 1997). Reichard and Hamilton (1997) also found vegetative reproduction was important for invader success. However, Cadotte and Lovett-Doust (2001) found that NIPS invading intact communities were not more likely to have clonal reproduction than native species in those same situations. Cadotte and Lovett-Doust conjectured that native perennial plants in these communities likely use clonal organs to compete with co-occurring native species. Our analyses show that abundant NIPS are more likely to have clonal growth, indicating that among NIPS, those with clonal growth may be better able to compete with pre-existing species.

Besides vegetative propagation via clonal growth, traits associated with sexual reproduction are also important for NIPS success. We showed that longer-flowering species are more likely to become abundant. Cadotte and Lovett-Doust (2001) also found, when comparing native and exotic species in southern Ontario, that NIPS (regardless of abundance status) were more likely to have longer flowering times. Longer-flowering species, especially those having continuous seed production or production at intervals through the growing season, are likely to benefit from environmental variability by being more likely to set seed during optimal conditions. This may be especially important for NIPS associated with disturbed habitats. "The disturbed" habitat was likely an ephemeral habitat type throughout much of these species' evolutionary history. Therefore, reproducing more often and longer may give individuals a better chance of colonizing new locations as they become disturbed.

The variable that was most strongly associated with NIPS abundance was native origin. Perhaps not surprisingly, species from Eurasia and Europe were more likely to become common when introduced in Ontario, and at the same time species from very different climates (the Mediterranean region, Asia proper, Africa, and tropical America) were significantly less likely to become com-

mon. The notion that native geography is important for subsequent invasion success has been commented on by a number of authors (Baker, 1986; Scott & Panetta, 1993; Williamson & Fitter, 1996; Goodwin, McAllister & Fahrig, 1999; Prinzing *et al.*, 2002). However, what seems interesting here is the fact that species native elsewhere in North America were not as likely to become common as those from Eurasia and Europe. Is there a general pattern of species evolving on a different continent being more successful invaders (given latitudinal and climatic overlap)? Exotics in Europe are over-represented by those originating from North America (Pyšek, Prach & Šmilauer, 1995; Weber, 1997), while in North America the reverse appears to be true (Cadotte & Lovett-Doust, 2001). Several possible reasons could account for why Eurasian and European species were more numerous and abundant than species from elsewhere in North America. First, species from the same continent may be phylogenetically more related. Species that are less phylogenetically related may be more likely to have evolved ecological novelties, which result in novel resource use (Webb, 2000). Second, as predicted by the so-called "enemy release hypothesis" (Mitchell & Power, 2003), exotic species may escape co-evolved herbivores or pathogens in their new habitats. Phylogenetically related taxa from the same continent may be less likely to find refuge among closely related taxa and their enemies. Finally, the pattern may simply be the result of a "sampling effect". Randomly selected species being introduced to a new region are more likely to be over-represented by a source having a larger pool of widely distributed species. Widely distributed species in North America are much more likely to be found in Ontario (as natives) than those from Europe. NIPS with large native ranges are more likely to become common than those having restricted ranges (Scott & Panetta, 1993; Williamson & Fitter, 1996; Goodwin, McAllister & Fahrig, 1999; Prinzing *et al.*, 2002).

Our analyses have revealed several general patterns in the NIPS of Ontario. Two significant steps remain. First, once further database analyses are compiled, our results can be compared to others to see how widespread these patterns are. Second, the general patterns found in this analysis do not uncover the mechanisms that cause the patterns (Cadotte, Murray & Lovett-Doust, 2006). We have listed several candidate hypotheses that may explain the observed patterns. More detailed analyses are needed to reveal actual mechanisms.

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APPENDIX I. Summary of the number of species for all variables used in the analyses.

Attribute	Variable	Number of species (percent)	Rare	
			SE1, 2 and 3	Common SE4 and 5
Time of introduction	pre-1952	846 (73.4)	516 (68.7)	272 (86.6)
	1952-1979	183 (15.9)	129 (17.2)	34 (10.8)
	after 1979	124 (10.8)	106 (14.1)	8 (2.6)
Abundance*	SEH	42 (5.0)		
	SE1	352 (41.6)		
	SE2	96 (11.3)		
	SE3	68 (8.0)		
	SE4	63 (7.4)		
	SE5	209 (24.7)		
	SEU	16 (1.9)		
Clonal organ	Present	118 (13.9)	64 (12.4)	52 (19.1)
	Absent	728 (86.1)	452 (87.6)	220 (80.9)
Flowering duration (months)	1	33 (5.7)	26 (7.9)	6 (2.8)
	2	137 (23.7)	93 (28.2)	39 (18.0)
	3	162 (28.1)	91 (27.6)	60 (27.6)
	4	161 (27.9)	81 (24.6)	72 (33.2)
	5	64 (11.1)	31 (9.4)	30 (13.8)
	6	16 (2.8)	6 (1.8)	8 (3.7)
	> 6	4 (0.7)	2 (0.6)	2 (0.9)
Flowering season	Early-season	52 (9.0)	35 (10.5)	15 (6.9)
	Mid-season	63 (10.9)	251 (75.6)	154 (70.6)
	Late-season	428 (73.8)	32 (9.6)	29 (13.3)
	All season	37 (6.4)	14 (4.2)	20 (9.2)
Geographic origin	Asia	72 (9.1)	51 (10.7)	18 (7.0)
	Eurasia	245 (31.1)	128 (26.8)	104 (40.6)
	Europe	264 (33.5)	147 (30.8)	101 (39.4)
	Mediterranean	21 (2.7)	18 (3.8)	0 (0.0)
	North America	158 (20.1)	111 (23.3)	31 (12.1)
	Tropical America	27 (3.4)	21 (4.4)	2 (0.8)
	Africa	1 (0.1)	1 (0.2)	0 (0.0)
Life Cycle	Annual (& biennial)	327 (39.9)	178 (36.0)	122 (45.2)
	Perennial	440 (53.7)	286 (57.8)	132 (48.9)
	Variable	53 (6.5)	31 (6.3)	16 (5.9)
Life-form	Herbaceous	722 (86.7)	427 (85.9)	243 (90)
	Shrub	62 (7.4)	40 (8.0)	9 (3.3)
	Tree	37 (4.4)	22 (4.4)	15 (5.6)
	Vine	12 (1.4)	8 (1.6)	3 (1.1)
Sex habit	Monoecious†	94 (11.9)	53 (10.4)	33 (12.1)
	Dioecious	25 (3.0)	16 (3.1)	8 (2.9)
	Hermaphrodite	712 (85.1)	439 (86.2)	227 (83.5)
	Polygynous	6 (0.2)	1 (0.2)	4 (1.5)
Soil moisture	Dry	71 (17.6)	45 (23.3)	16 (10.1)
	Moist-dry	24 (6.0)	14 (7.2)	9 (5.7)
	Moist	125 (31.1)	73 (37.8)	38 (23.9)
	Moist-wet	17 (4.2)	9 (4.7)	5 (3.1)
	Wet	43 (10.7)	19 (9.8)	14 (8.8)
	Variable	122 (30.4)	33 (17.1)	77 (48.4)

*All variables here and below are for species introduced prior to 1952. SEH: historical records but no recent confirmation; SEU: status unknown.

†Includes andromonoecious and gynomonocious.