Journal of Applied Ecology 2006
43, 43–50

Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal

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Summary

1. Attempts to quantify the impact of non-native plants on the vegetation of invaded habitats have often been criticized because of the frequent use of observational assessments (invaded/uninvaded comparisons) focused on local- rather than community-level effects. This study highlights how removal experiments combined with partitioning of diversity components across spatial scales can provide key insights into invasive species' impacts.

2. *Impatiens glandulifera* (Balsaminaceae) is a widespread invasive riparian weed, yet few quantitative assessments of its impact on natural vegetation exist. Thus replicated experiments were used to compare the impact of *Impatiens* removal on α, β, γ components of species richness, diversity and evenness in open riparian habitats in north-east England.

3. Plant community response to *Impatiens* removal was rapid, with a significant increase in seedling recruitment resulting in an average increase of four species m^{-2}. The impact of *Impatiens* invasion was most marked for light-demanding species. Eight non-native species (in addition to *Impatiens*) occurred in the community and these responded proportionally more to *Impatiens* removal than native species. As a result the proportion of non-native species in removal plots was higher than in invaded plots.

4. The increase in α richness and diversity following *Impatiens* removal was matched by a similar increase in the γ components. Thus the effect of *Impatiens* was significant at both the local plot scale and at the scale of the riparian community, although the former effect was more marked. Species accumulation curves suggested that extensive *Impatiens* stands may reduce species richness by as much as 25%.

5. *Synthesis and applications.* Removal experiments appear particularly well suited to assess the impacts of herbaceous non-native plants on ruderal communities. By partitioning diversity components, impacts were consistently assessed at local and community scales and, when combined with analysis of species accumulation curves, provided a comprehensive assessment of impact on the plant community. The approach adopted in this study highlights that although *Impatiens* reduces native species diversity in open and frequently disturbed riparian vegetation, many of the species negatively influenced by *Impatiens* are widespread ruderal species. Furthermore, management may lead to a compensatory increase in the abundance of other non-native species and thus fail to achieve desired conservation goals.

Key-words: alien species, biodiversity, biological invasions, community ecology, removal experiment

Journal of Applied Ecology (2006) **43**, 43–50
doi: 10.1111/j.1365-2664.2005.01102.x

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Introduction

Considerable concern exists regarding the potential for invasive plant species to threaten the species composition and community structure of native habitats (Cronk & Fuller 1995; Manchester & Bullock 2000; Weber 2003). However, in contrast to the voluminous literature documenting increasing numbers and expanding ranges of non-native species in world floras (Lonsdale 1999; Pyšek & Hulme 2005), quantitative assessments of impacts on biodiversity are far less comprehensive (Hulme 2003). Addressing this information deficit is widely recognized as an international research priority (Parker *et al*. 1999; Byers *et al*. 2002). Current understanding of invasive plant impacts is drawn largely from observational studies that have compared invaded and uninvaded habitats (Levine *et al*. 2003). However, as species diversity may in itself influence the likelihood of invasion, separating cause and effect using such correlative approaches is particularly difficult (Levine & D'Antonio 1999). Alternative approaches include either the experimental introduction or removal of invasive species. Understandably, experimental introductions of invasive species into semi-natural habitats are not encouraged. Conversely, removal experiments present substantial opportunities for assessing the ecosystem consequences of plant invasions (Zavaleta, Hobbs & Mooney 2001). Although potentially a powerful approach, indirect effects of species removal (e.g. soil disturbance) may obscure the true impact of a specific invasive species (Diaz *et al*. 2003). However, these indirect effects of species removal are expected to be less severe in early successional communities naturally exposed to relatively high levels of disturbance.

Riparian habitats are particularly vulnerable to plant invasions, partly as a result of naturally high disturbance frequencies (Pyšek & Prach 1993; Hood & Naiman 2000). *Impatiens glandulifera* Royle (Balsaminaceae) is a widespread invasive annual frequently included in compendia of globally important non-native plants that invade natural habitats (Cronk & Fuller 1995; Weber 2003). Although native to the western Himalayas, *I. glandulifera* (hereafter referred to as *Impatiens*) has become naturalized in northern and central Europe, temperate North America and New Zealand (Weber 2003). It is ranked in the top 20 invasive plants in the UK (Crawley 1987), occurs on the Swiss 'black list' of harmful invasive species (Anonymous 2002) and is one of the invasive species in Germany against which specific control measures are directed (Kowarik 2003). Given its notoriety, it is surprising that few quantitative assessments of its impact on natural vegetation have been published. Apart from experimental evidence that *Impatiens* may compete successfully with native plants for pollinators (Chittka & Schürkens 2001), observational studies indicate impacts may largely consist of a local change in cover and/or dominance of native species (Larson & Martinson 1998; Maule *et al*. 2000).

In order to address the impact of *Impatiens* on native plant species richness, replicated *Impatiens* removal experiments were undertaken in riparian habitats of north-east England. The experiments aimed to assess the magnitude and direction of changes in species diversity as a result of *Impatiens* removal. Species diversity has two components: richness and evenness (Stirling & Wilsey 2001). The focus of invasive species impacts has been primarily on richness (Levine *et al*. 2003) yet changes in species evenness may influence invasion resistance, productivity and local plant extinction rates (Wilsey & Potvin 2000; Smith *et al*. 2004). In addition, impacts on species diversity should be assessed at both the local (sample) and habitat scales (Gering, Crist & Veetch 2003). In order to facilitate comparison of impacts on diversity at local and habitat scales, additive partitioning of species diversity components (Lande 1996) can be used to separate total diversity drawn from several samples (γ diversity) into the additive components α (mean within-sample diversity) and β (between-sample heterogeneity). The relative proportion of β diversity (β/γ) provides a useful comparator of between-sample heterogeneity (Crist *et al*. 2003). The concepts of α, β, γ diversity are based on consideration of the spatial scales at which different processes might dominate, but there is no prescription in ecology on how to define the local and regional communities (Loreau 2000). This study thus adopts additive partitioning of diversity components to address the impacts of invasive species at local and habitat scales, but the approach could be extended to landscape and regional scales. The possibility exists that local dominance of an invasive plant may reduce α components but increase turnover between plots (β) such that community diversity (γ) is unchanged by invasion. However, assuming *Impatiens* has a significant impact, it was expected that α, β, and γ diversity would be higher in plots where the invader had been removed.

Materials and methods

Experimental plots were established along the River Wear in Durham City, north-east England (NZ 286416), UK. Although Durham City is in the lowlands, the River Wear drains an upland catchment and is prone to periodic exceptional flows following heavy rains that have resulted in at least six significant flood events in the 20th century. *Impatiens* was first recorded on the riverbanks of Durham City in 1900 and thus is likely to have become integrated into the riparian vegetation (Collingham *et al*. 2000). Twelve sites were established within 2 km of each other, each representative of herbaceous riparian plant communities. These included inundation communities, mesotrophic grassland and fen, habitats that are typically invaded by *Impatiens* (Graham 1988). In each site, a single relatively homogeneous stand of *Impatiens* was selected in mid-May, a period after which much of the natural intraspecific self-thinning has occurred and densities have stabilized (Prowse 1998). Each stand was a sufficient size to accommodate two paired plots, each 1 m^2 and separated by at least 1 m (but rarely more than 5 m). Plot size was adequate for sampling relatively species-poor herbaceous plant communities (Cain & Castro 1959). One plot of each pair was randomly assigned to a removal treatment, while the remaining reference plot was left unmanipulated. The removal treatment consisted of individually cutting and removing all *Impatiens* stems by hand at ground level. The treatment was applied within the 1-m^2 plot and also in a 0·5-m buffer strip around the plot to minimize edge effects from neighbouring *Impatiens* plants. No re-establishment of *Impatiens* occurred in the removal plots during the 4-month study. The reference plot was undisturbed but was positioned to ensure that it was no closer than 0·5 m from the perimeter of the *Impatiens* stand. An effort was made to ensure reference plots at each site had similarly high *Impatiens* cover (80–100%). As a result, photon flux density (660 nm) at ground level in the removal plots was more than twice as high as in the reference plots (2·45 vs. 1·18 μmol s^{-1} m^{-2}, respectively, paired $t = 2{\cdot}58$, d.f. 11, $P < 0{\cdot}05$). Vegetation composition was assessed using frequency measures for individual species. Each plot was divided into 25 cells (each 20 × 20 cm) and the presence and absence of species in each cell recorded. In addition, total counts of unidentified seedlings were undertaken to assess the impact of removal on recruitment. Assessments were undertaken three times between June and August. Nomenclature and species status follows Preston, Pearman & Dines (2002)

Following Martin, Moloney, & Wilsey (2005), species diversity (α and γ) was calculated using Simpson's reciprocal index of diversity 1/D ($D = \Sigma\,[n_i/N]^2$, where n_i is the frequency of each species and N is the total frequency of all species). Simpson's index has been shown to be robust for small sample sizes even where species richness is high (Lande 1996). Species diversity was separated into richness (S) and evenness (E) components. Evenness was calculated as $E_{1/D} = (1/D)/S$ as it is mathematically independent of richness (Smith & Wilson 1996). Gamma (γ) diversity was partitioned into α and β using the 1 – D form of Simpson's index (hereafter referred to as 1 – D) and S because of their desirable statistical properties when additively partitioned (Lande 1996). Beta diversity (β) was calculated by subtracting α from γ (Lande 1996). Alpha (α) diversity was estimated as the mean number of species across all 24 plots, as well as separately for the 12 removal and 12 reference plots. Gamma diversity was estimated as the total species number across all 24 plots, and separately for the 12 removal and 12 reference plots. To facilitate direct comparisons of the plots, data regarding *Impatiens* frequency were not included in the diversity analyses. However, changes in the distribution and abundance of other non-native species were contrasted with those of native species. To account for pairing, analyses were undertaken on the difference between paired plots for each diversity measure. Repeated-measures ANOVA in SAS v8·2 (SAS Institute Inc., Cary, NC) were undertaken for each variable with time as the repeated measure. To aid interpretation of the diversity measures, species abundance (the average number of cells a species occupied within a plot) and species frequency (the number of plots in which a species occurred) were also calculated.

Within a homogeneous habitat, as sampling intensity increases, γ richness will also increase towards an asymptote. If sample size is insufficient, it may not be possible to distinguish differences in species diversity in two contrasting samples (Gotelli & Colwell 2001). Species' accumulation curves provide a means to assess sampling efficiency as well as estimate a more robust measure of γ richness. Species' accumulation curves generate a negatively biased estimate of species richness and a range of non-parametric methods exist to counter the bias when estimating species richness from samples (Colwell & Coddington 1994). No rules exist as to which estimate is more reliable for different assessments, but Burnham and Overton's second-order jackknife provides a relatively unbiased estimate of species richness for small sample sizes (Colwell & Coddington 1994; Chiarucci *et al.* 2003). The second-order jackknife was used to assess the relative sampling efficiency and estimate total species richness in the removal and reference treatments.

Results

Significant correlations in α richness existed between corresponding pairs of plots ($r_s = 0{\cdot}785$, 0·754, 0·718, all d.f. 10, $P < 0{\cdot}01$ for June, July and August, respectively; for June see Fig. 1a) and reflected the trend in native ($r_s = 0{\cdot}893$, 0·692, 0·763, all d.f. 10, $P < 0{\cdot}01$) rather than non-native species ($r_s = 0{\cdot}270$, 0·378, 0·408, all d.f. 10, $P > 0{\cdot}05$). *Impatiens* significantly reduced both the mean abundance of species within plots (2·68 vs. 3·94 cells species^{-1}, paired $t = 2{\cdot}41$, d.f. 47, $P < 0{\cdot}05$) and their frequency between plots (2·02 vs. 2·92 plots species^{-1}, paired $t = 3{\cdot}38$, d.f. 47, $P < 0{\cdot}005$) but the species ranking remained similar in both cases (Fig. 1b,c). The majority of species were scarce and occurred in less than one-quarter of the plots. The widespread species that were found in more than half of all plots included *Aegopodium podagraria*, *Elytrigia repens*, *Calystegia sepium*, *Galium aparine* and *Lamium album*. Many species were able to spread vegetatively and thus, while individual species counts per plot were low, vegetation cover was usually greater than 100%. A significant positive relationship existed between mean abundance and frequency for species in plots where *Impatiens* was removed ($r_s = 0{\cdot}366$, d.f. 42, $P < 0{\cdot}05$) but not where it was present ($r_s = 0{\cdot}345$, d.f. 30, $P > 0{\cdot}05$).

Removal of *Impatiens* led to a significant increase in species richness, resulting in an average of four additional species per plot ($F_{1,55} = 54{\cdot}82$, $P < 0{\cdot}0001$; Table 1).

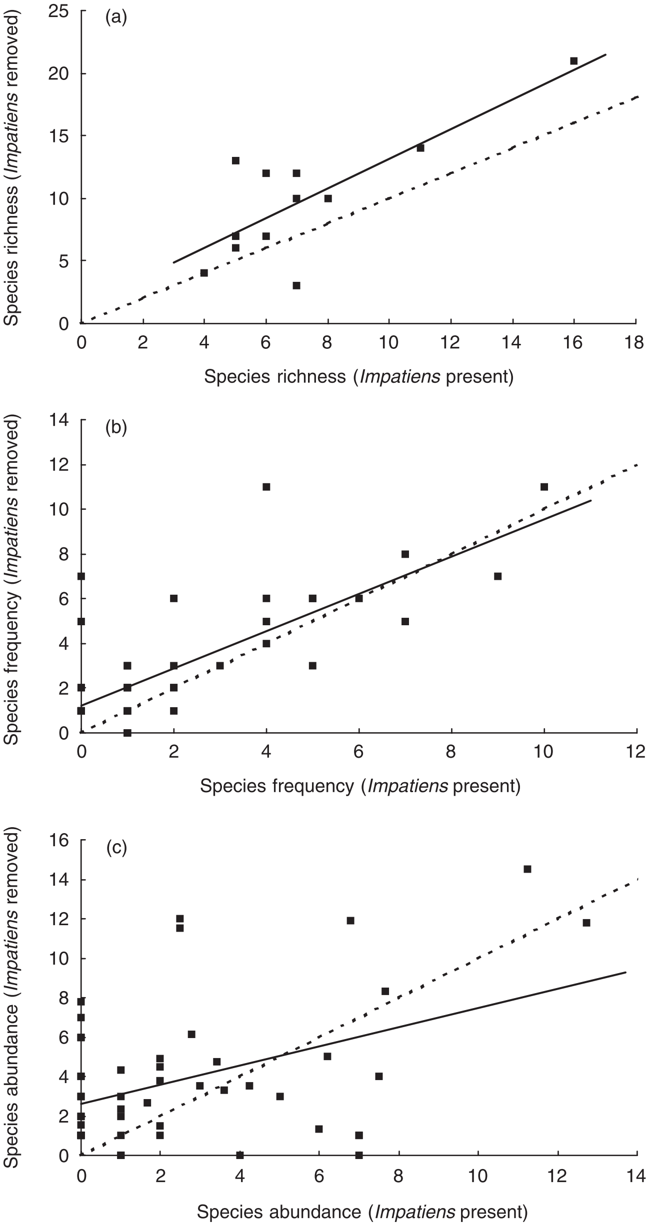

Fig. 1. Significant positive relationships in species richness, frequency and abundance in plots where *Impatiens glandulifera* is present or experimentally removed. (a) Linear relationship in species richness between paired plots in June, $y = 1{\cdot}18x + 1{\cdot}34$, $R^2 = 0{\cdot}617$, $F_{1,10} = 16{\cdot}08$, $P < 0{\cdot}005$. (b) Linear relationship between frequency in each paired plot for each species, $y = 0{\cdot}83x + 1{\cdot}24$, $R^2 = 0{\cdot}581$, $F_{1,46} = 63{\cdot}78$, $P < 0{\cdot}001$. (c) Linear relationship between abundance across all plots for each species, $y = 0{\cdot}48x + 2{\cdot}64$, $R^2 = 0{\cdot}180$, $F_{1,46} = 10{\cdot}36$, $P < 0{\cdot}005$. Dotted line is that of equality, $y = x$.

The significant difference in seedling density between plots with and without *Impatiens* indicated that many of the additional species were new recruits ($F_{1,55} = 49{\cdot}90$, $P < 0{\cdot}0001$; Fig. 2). The additional species resulted in a significant increase in α diversity ($F_{1,55} = 28{\cdot}61$, $P < 0{\cdot}0001$; Table 1) but a decline in α evenness in removal plots ($F_{1,55} = 4{\cdot}70$, $P < 0{\cdot}05$; Table 1). Where *Impatiens* was removed, α richness ($F_{1,55} = 54{\cdot}55$, $P < 0{\cdot}0001$; Fig. 1a) and diversity ($F_{1,55} = 31{\cdot}00$, $P < 0{\cdot}0001$; Table 1) of other non-native species increased significantly but their evenness declined ($F_{1,55} = 8{\cdot}74$, $P < 0{\cdot}005$; Table 1). A similar pattern was found for native species except that in this case no difference in evenness was found in plots with or without *Impatiens* ($F_{1,55} = 0{\cdot}01$, $P > 0{\cdot}05$; Table 1). Non-native species accounted for more than one-third of the additional species found in removal plots. The non-native species that benefited most from *Impatiens* removal included the widespread perennial herbs *Lamium album*, *Myrrhis odourata*, *Petasites fragrans* and *Tanacetum parthenium*. Consequently, removal plots had a significantly higher proportion of non-native species than those where *Impatiens* was present (33·53% vs. 26·68%, respectively, $F_{1,55} = 9{\cdot}90$, $P < 0{\cdot}005$; Table 1).

A total of 47 species was recorded across all plots, with almost 90% of taxa occurring in plots where *Impatiens* was removed whereas fewer than two-thirds were found in invaded plots. Four species were never found in removal plots (*Geum urbanum*, *Lathyrus pratensis*,

Table 1. Mean (± SE) species richness, Simpson's reciprocal index of diversity and Simpson's evenness index in June, July and August for experimental plots where *Impatiens* was removed or present. Values are presented for all species and separately for native and non-native species

	All species		Native species		Non-native species	
	Removed	Present	Removed	Present	Removed	Present
Richness						
June	9·92 ± 1·44	7·25 ± 0·95	6·83 ± 1·08	5·50 ± 0·72	3·08 ± 0·48	1·75 ± 0·30
July	11·17 ± 1·55	7·25 ± 0·79	7·75 ± 1·29	5·17 ± 0·63	3·42 ± 0·36	2·08 ± 0·31
August	11·08 ± 1·33	7·08 ± 0·86	7·42 ± 1·11	5·25 ± 0·64	3·67 ± 0·33	1·83 ± 0·30
Diversity						
June	5·78 ± 0·72	4·18 ± 0·42	4·20 ± 0·46	3·19 ± 0·26	2·09 ± 0·33	1·48 ± 0·25
July	5·92 ± 0·71	4·42 ± 0·35	4·36 ± 0·44	3·29 ± 0·32	2·35 ± 0·30	1·65 ± 0·19
August	5·73 ± 0·77	4·11 ± 0·45	4·30 ± 0·50	3·34 ± 0·35	2·31 ± 0·31	1·29 ± 0·17
Evenness						
June	0·62 ± 0·05	0·61 ± 0·04	0·69 ± 0·05	0·62 ± 0·04	0·65 ± 0·08	0·80 ± 0·08
July	0·54 ± 0·03	0·65 ± 0·05	0·63 ± 0·05	0·68 ± 0·05	0·68 ± 0·04	0·86 ± 0·05
August	0·52 ± 0·03	0·59 ± 0·04	0·65 ± 0·06	0·66 ± 0·04	0·61 ± 0·04	0·76 ± 0·09

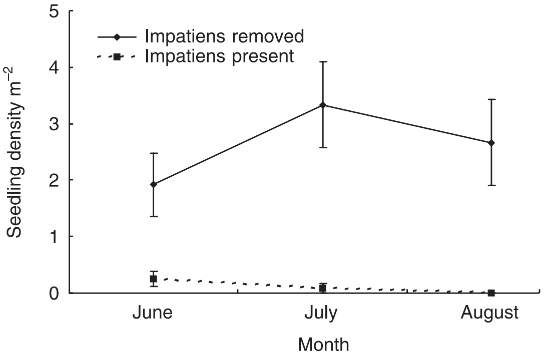

Fig. 2. Seedling density in plots with and without *Impatiens glandulifera* in each of three sampling periods.

Tanacetum vulgare and *Vicia cracca*) whereas 16 species were only found in the removal plots. The species exhibiting the most marked response were *Agrostis stolonifera* and *Tanacetum parthenium*, which, while never found in the invaded plots, appeared in approximately half the removal plots. A significant positive correlation existed between the mean change in abundance between the treatments and species' Ellenberg light scores (r_s = 0·296, d.f. 43, P < 0·05). Approximately three-quarters of species richness was partitioned into the β components ($\beta = \gamma - \alpha$) in both the removal (73·60%) and invaded plots (75·30%). In contrast, species diversity was mostly partitioned into the α component and proportionally more so in the removal (82·15%) than invaded plots (72·50%). This would suggest a stronger local effect by *Impatiens* on rare than widespread species. The presence of an asymptote in the species accumulation curves indicated that the sampling intensity was sufficient to capture the majority of species richness of the herbaceous riparian vegetation in the study area (Fig. 3a). Estimates of maximum species richness continued to emphasize higher richness when *Impatiens* was removed (56–64 species) than when present (39–41 species), although this difference was less marked when only native species were considered (Fig. 3b).

Discussion

Removal experiments provide a useful tool in the assessment of invasive species' impacts but may not entirely reflect the effect of species' introductions (Diaz *et al.* 2003). Although removing an annual species from a frequently disturbed habitat should limit the indirect effects of any experimental manipulation, the subsequent vegetation response may still be constrained. The vegetation response in removal plots will be limited to recruitment from the seed bank, colonization from the seed rain, vegetative expansion from outside the plot and changes in cover within the plot. It is therefore possible that some species vulnerable to *Impatiens* invasion would not have been recorded from the removal plots. However, species that did not possess a seed bank, were not setting seed or had poor lateral spread were rare in the riparian vegetation, composed as it was of many ruderal species. The relative speed of the response, with significant changes in removal plots being found within 1 month of the treatment, and subsequent limited change in species diversity and/or richness suggest the length of the study adequately captured the magnitude of the response. The limited temporal variation in response suggests that observed trends did not appear to reflect species succession. It can therefore be tentatively concluded that the patterns identified in this study probably are representative of the impacts of *Impatiens* in open riparian vegetation.

Impatiens is the tallest annual in the UK, reaching up to 2·5 m in height and often forming dense even-aged stands (Beerling & Perrins 1993; Willis & Hulme 2004). As a consequence, the shade it casts reduces germination and establishment of other species beneath its canopy, with a resultant reduction in species richness. Light-demanding species appeared to respond more

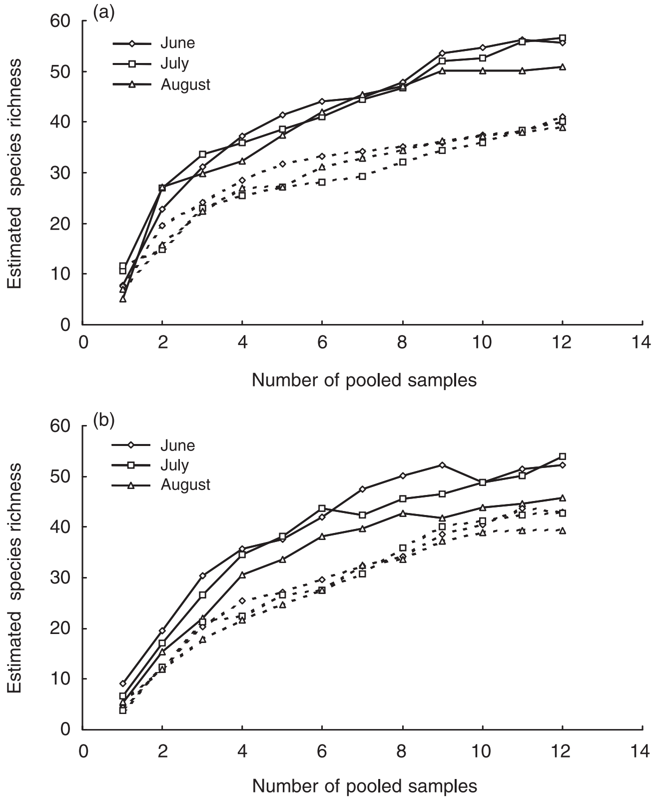

Fig. 3. Species accumulation curves estimated using Burnham and Overton's second-order jack-knife procedure for plots with (dashed line) and without (entire line) *Impatiens glandulifera* in each of three sampling periods. (a) Accumulation curve for all species; (b) accumulation curve for native species only.

strongly to *Impatiens* removal. In the present study the presence of *Impatiens* resulted in more than a 25% reduction in α richness and diversity. Evenness was less responsive to *Impatiens* removal, but did decline as additional species subsequently colonized removal plots. The finding that additive partitions of species richness had a high β component while partitions of Simpson's diversity had a high α component is expected because of the generality of the distribution–abundance relationship (Crist *et al.* 2003). The partitioning of species richness components was similar for the removal and reference plots, but a greater proportion of diversity was partitioned into the α component in plots where *Impatiens* was removed. At the scale of the habitat, the total number of species encountered across all plots with *Impatiens* was 30% lower than where *Impatiens* was removed. However, second-order jack-knife estimates of richness presented a more conservative 25% reduction. Thus the effect of *Impatiens* is significant at both the local plot scale and at the scale of the riparian community, although the former effect is more marked. Light-demanding species in the regional pool tend to be rare or absent from plots where *Impatiens* is present.

The results support anecdotal and observational studies suggesting *Impatiens* has a negative impact on the plant diversity of riparian grassland habitats (Beerling & Perrins 1993; Dawson & Holland 1999). The study sites in Durham City were not atypical of the open riparian habitats where *Impatiens* is frequently found (Graham 1988; Willis, Hulme & Huntley 1997; Dawson & Holland 1999). The riparian habitats of north-east England appear particularly vulnerable to *Impatiens* invasion (Dawson & Holland 1999; Willis & Hulme 2002) and a survey of 730 500-m stretches of the River Wear identified *Impatiens* in more than 75% of samples (Willis, Hulme & Huntley 1997). The consequence of invasion by *Impatiens* in these plant communities was the loss of approximately four species m^{-2} up to a maximum of around 15 species where *Impatiens* is extensively distributed. However, all of the species encountered in the plots are widespread in the UK and thus the threat to any individual species from *Impatiens* may be small. Furthermore, in the absence of *Impatiens* other non-native species may comprise a greater proportion of the vegetation, several of which (e.g. *Aegopodium podagraria* and *Myrrhis odourata*) may also exclude native species.

This study has highlighted some of the problems in assessing impacts of invasive species (Hulme 2003). *Impatiens* is widespread in the UK and frequent in human-modified environments, resulting in a high public profile. Fewer species are found beneath its canopy; however, in open and frequently disturbed riparian vegetation, many of the species negatively influenced by *Impatiens* are widespread ruderal species. Thus while several authors recommend its removal (Beerling & Perrins 1993; Dawson & Holland 1999) such action may only lead to a compensatory increase in the abundance of other non-native species and thus fail to achieve desired conservation goals. Under such circumstances managing the community to reduce invasion impacts may be more effective (Bakker & Wilson 2004; Perry, Galatowitsch & Rosen 2004). Furthermore, control strategies for *Impatiens* are rarely effective in the long term (Wadsworth *et al*. 2000). However, focusing management where *Impatiens* populations are most extensive may not only improve the effectiveness of control (Wadsworth *et al*. 2000) but, as this study has shown, also deliver the greatest potential benefits to biodiversity.

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Received 5 May 2005; final copy received 3 August 2005
Editor: Rob Freckleton