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Plant functional traits suggest novel ecological strategy for an invasive shrub in an understorey woody plant community

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Summary

1. Understanding ecological strategies of invasive species relative to the entire native community is important in understanding and managing both the mechanisms and the potential impacts of invasion, but few studies have taken this approach.

2. We utilize advances in plant ecology to compare functional traits of an invasive shrub species, autumn-olive *Elaeagnus umbellata*, to those of the understorey native woody plant community in a southeast Michigan forest. We estimate species trait distributions for six leaf functional traits (specific leaf area, leaf laminar area, leaf dry matter content, leaf nitrogen content, leaf carbon: nitrogen ratio and delta ^{15}N) using a kernel estimator. We then use pairwise trait distance and overlaps to describe the ecological strategy of the invasive shrub relative to that of the native understorey woody plant community.

3. The overlap of the invasive shrub's trait distribution with those of the native species was found to be smaller than the overlap of a native shrub's distribution with other native species, consistent with the empty niche hypothesis of invasion. However, the invasive species' mean leaf functional trait values typically fall outside of the range of most native species' mean trait values, suggesting the invasive shrub extends trait space for understorey individuals of the native woody plant community.

4. The invasive shrub's leaf trait values are characteristic of a sun-demanding species, contradicting its presence in the shaded forest understorey community and its persistence in an empty niche. We propose that this novel use of leaf functional traits by the invasive shrub could indicate that the invasion is facilitated by additional mechanisms such as release from natural enemies, association with nitrogen-fixing bacteria, use of an empty temporal niche (namely the light available to the understorey early in the growing season), bird dispersal or some synthesis of these factors.

5. *Synthesis and applications*. This study develops plant functional trait theory by studying an invasive species within the context of the entire native woody plant community. The approach can improve our understanding of the potential mechanisms of an invasion event and suggest ecological consequences and related management strategies for the maintenance of native forest communities. Specifically, this study, along with known data on the invasive species, suggests aggressive management in sunny gap and edge habitat provides the best strategy for long-term control.

Key-words: community invasion, empty niche hypothesis, functional traits, trait overlap

Introduction

Invasive species present a substantial threat to ecological communities (Mack *et al.* 2000). A deeper understanding of the mechanisms leading to invasion and their relative importance in specific contexts may help to mitigate losses of biodiversity and ecosystem function. It would also lead to more reliable predictions of those species likely to invade a community and of invasion impacts. Many hypotheses have been proposed to explain invasiveness (reviewed by Theoharides & Dukes 2007), including the empty niche hypothesis (e.g. Hierro, Maron & Callaway 2005), enemy release hypothesis (e.g. Maron & Vilá

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2001; Keane & Crawley 2002; Dewalt, Denslow & Ickes 2004), novel weapons hypothesis (e.g. Callaway & Ridenour 2004) and various fitness trade-off mechanisms dictated by the ecological strategy of the exotic species and the composition of the native community (e.g. Shea & Chesson 2002; MacDougall, Gilbert & Levine 2009). Species traits have been correlated with increased likelihood of invasion; for instance, superior colonizing potential allows invasion of disturbed habitats, but few studies have established a link between these traits and specific mechanisms of invasion (Harrington, Brown & Reich 1989; reviewed by Pyšek & Richardson 2007). Here, we suggest that advances in plant functional ecology can establish this link by considering traits of the invasive species in the context of traits of the native species. We apply these methods to the invasion of a closed canopy forest understorey by an exotic shrub species.

Functional traits reflect a species' interactions with the biotic and abiotic environment (Reich *et al.* 2003; McGill *et al.* 2006). These traits demonstrate differences in resource use and life-history strategy among plants, reflecting important fundamental niche axes along which species are differentiated (Westoby *et al.* 2002; Violle & Jiang 2009). For example, variation in certain leaf characteristics reveals trade-offs involving photosynthetic carbon fixation in plant species, known as the leaf economics spectrum (Wright *et al.* 2004; Westoby & Wright 2006). Variation in other leaf traits may reflect trade-offs between herbivore resistance, tolerance and photosynthetic capacity, with corresponding effects on the dynamics of understorey plants (e.g. Bryant, Chapin & Klein 1983; Shearer & Kohl 1986; Spriggs, Stock & Dakora 2003; Hobbie & Hobbie 2008). Patterns in species' functional traits are increasingly being used to understand the mechanisms of community assembly, particularly in plant communities; patterns of habitat filtering as well as trait overdispersion from competitive pressure have frequently been documented (e.g. Weiher, Clarke & Keddy 1998; Stubbs & Wilson 2004; Ackerly & Cornwell 2007; Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009).

Ecologists have used traits to demonstrate high functional dissimilarity of successful invaders with the dominant plant species (Emery 2007) and have identified traits that are similar among invasive species in a similar region or habitat (Kolar & Lodge 2001; Lloret *et al.* 2005), or more common among invasives than natives (Rejmánek & Richardson 1996; Williamson & Fitter 1996; Grotkopp, Rejmánek & Rost 2002; Kyle & Leishman 2009). Often these studies are limited by their species-specific investigations and generalizations must be carefully considered. Largely, these studies categorize species based on broad functional groups or do not link functional traits to the biotic and abiotic filters (Pyšek & Richardson 2007; Theoharides & Dukes 2007). Here, we compare the leaf functional trait distributions of an invasive species with those of each native species in the understorey of a temperate forest tree community.

We study the invasion of autumn-olive *Elaeagnus umbellata* Thunb., an invasive shrub described as shade intolerant (Catling *et al.* 1997), into the understorey of a closed canopy forest in southeast Michigan. However, based on demographic analyses (see Appendix S1), we know that *E. umbellata* is growing and increasing in population in the understorey. Throughout this article, references to 'the invasive species' refer to *E. umbellata*. As with any closed canopy forest, we expect light availability to be a key driver of woody plant dynamics (Pacala *et al.* 1996; Kobe 1999); in the light of the apparent contradiction of the presence and persistence of *E. umbellata* in the understorey, we are especially interested in exploring traits related to light availability. Therefore, we use the distribution of a series of morphological and chemical leaf traits in understanding ecological strategies of the native and invasive species and ask two key questions linking traits to the mechanisms of invasion: (i) Does the invasive occupy an empty niche in this community, evidenced by demonstrating a range of traits not otherwise found in the native community, or is it competing more directly with native species that use a similar range of trait space? To answer this question, we use the distribution of leaf traits across leaves and individuals of the invasive and the native species (rather than just spacing of species' mean trait values) and quantify the overlap in species' trait distributions. Recent studies have highlighted the potential importance of functional traits and the information about species interactions that can be revealed through patterns of overlap between species' trait distributions (Mouillot *et al.* 2005; McGill *et al.* 2006; Lake & Ostling 2009). (ii) Is the invasive shrub exhibiting a suite of traits that is novel in the community somehow (beyond taking advantage of unused trait space)? Specifically, is it expanding existing community trait space and in what direction? If the invasive exploits unused trait space, the way in which it does so should provide information about the potential mechanisms of invasion. We examine the position of the invasive's mean value of each trait relative to the rest of the community. In carrying out the analyses, we consider the invasive in the context of the entire native woody understorey plant community and compare its trait relationship with the community to the trait relationship of witch-hazel *Hamamelis virginiana* L., the only native shrub at this site, with the other native species in the community.

Materials and methods

Research was conducted at the University of Michigan's E.S. George Reserve in Livingston County, MI, USA (42°27′24·36″N, 84°00′40·03″W). The 525 ha reserve was farmed prior to 1927, when it was established as a game reserve. Within a few years, it was converted to a wildlife sanctuary and research area with minimal human intervention. We worked with an existing 16 ha inventory plot comprised of mid- to late-secondary closed canopy forest dominated by *Quercus* spp., *Acer* spp. and *Carya* spp. (Allen, Vandermeer & Perfecto 2009). The site has not had extensive disturbance since its establishment as a reserve, except for typical local tree falls. The soil is formed from glacial till and is generally loam to sand (Boyer-Ohtonen), with no qualitative difference across the site. The site is generally well drained, which suggests that despite a relatively nutrient-rich A-horizon, most of the soil is nutrient poor. All woody

Table 1. Species names, codes and number of stems sampled

Scientific name	Common name	Code	Class	Number of individuals sampled
Acer rubrum L.	Red maple	Ar	Canopy tree	47
Amelanchier arborea (Michx.) Fernald	Serviceberry	Aa	Understorey tree	23
Carya glabra (Miller) Sweet	Pignut hickory	Cg	Canopy tree	5
Cornus florida L.	Flowering dogwood	Cf	Understorey tree	4
Elaeagnus umbellata Thunb.	Autumn-olive	Eu	Invasive shrub	59
Hamamelis virginiana L.	Witch-hazel	Hv	Native shrub	55
Prunus serotina Ehrhart	Black cherry	Ps	Canopy tree	37
Prunus virginiana L.	Choke cherry	Pv	Understorey tree	2
Quercus alba L.	White oak	Qa	Canopy tree	2
Quercus velutina L.	Black oak	Qv	Canopy tree	4
Sassafras albidum (Nuttall) Nees	Sassafras	Sa	Understorey tree	2
Ulmus americana L.	American elm	Ua	Understorey tree	3

plants > 3·18 cm dbh have been mapped, identified, measured and tracked for 5 years. In addition, we sampled traits from individuals between 1·00–3·18 cm dbh within a 1 ha subplot of the forest to focus on the regeneration stage of these species, where competition among individuals is likely to be more intense and survivorship is lowest. We sampled from all individuals of rarer species and selected no more than 60 individuals of common species to sample (see Table 1 for sample sizes). All 11 native woody species present in the understorey were sampled. The sampled forest area was closed canopy forest, limiting the range of light environment sampled to that found in forest understorey.

TARGET SPECIES

The invasive shrub *E. umbellata* is established in temperate forests of the eastern and midwestern United States. *Elaeagnus umbellata* is native to the sub-Himalayan regions of northern Pakistan, as well as China, India, Japan and Korea (Ahmad, Sabir & Zubair 2006). In its native range, *E. umbellata* tolerates a large variation of pH (4–8) and soil moisture content ranging from drought to swampy conditions, with similar variation in morphological characteristics among ecotypes (Ahmad, Sabir & Zubair 2006). Seeds are contained in nutrient-rich fruits, which are dispersed by birds (Ahmad, Sabir & Zubair 2006; LaFleur, Rubega & Elphick 2007). It is both allelopathic (Orr, Rudgers & Clay 2005) and nitrogen fixing (Catling *et al*. 1997; Goldstein *et al*. 2010) and has been observed to persist in monotypic stands in open, nutrient-limited habitats. However, *E. umbellata* has been observed in limited light conditions in introduced habitat (Orr, Rudgers & Clay 2005), persisting in both edge and interior habitat (Yates, Levia & Williams 2004). As *E. umbellata* is found beneath the canopy in our study site, these understorey populations were the focus of this study.

Elaeagnus umbellata was first observed at the George Reserve in the early 1980s (F.C. Evans, personal communication; E.E. Werner, personal communication). It is now prolific in open grasslands, along roads, and in forest edge habitat at the study site. It is persisting in the understorey with 11 other native woody plant species in various life-history stages.

TRAITS MEASURED

Traits were chosen for their association with established strategy axes or other key functions. Several of these traits are explicitly linked to competition for light, one of the most limiting resources in a closed canopy forest (e.g. Finzi & Canham 2000). In all, we selected three morphological and three chemical traits, representing the leaf economic spectrum, the leaf size–twig size trade-off axis, foliar defence and nutrient uptake. The three morphological traits chosen were specific leaf area (SLA), leaf dry matter content (LDMC) and leaf laminar area (LA). SLA measures the surface area of an individual leaf relative to its mass. This trait is linked to relative growth rate, is key to the leaf economic spectrum and gives an indication of the light conditions under which a species tends to persist (the adaptive response of species) – full sun (high SLA) to shade (low SLA) (Reich, Walters & Ellsworth 1997; Wright *et al*. 2004). SLA has also been shown to vary with resource availability (Chapin 1980), although our analyses assume that resources are constant across the community. LDMC, the ratio of dry to wet mass of a leaf, indicating the structural investment in a leaf, is associated with leaf thickness and is a partial reflection of biomechanical resistance to physical damage (Cornelissen *et al*. 2003). LA measures the available surface area for photosynthesis and transpiration, affects the heat or energy balance of leaves and is a key component of the leaf size–twig size spectrum (Westoby & Wright 2003). This is not a direct measurement of fitness or resource utilization but may indicate differences in total leaf area or light preferences among co-occurring species. We measured these leaf morphological traits for *E. umbellata* and all 11 native woody species. The three chemical traits chosen were leaf nitrogen concentration (N_{mass}), carbon/nitrogen ratio (C:N ratio) and the natural ^{15}N abundance (delta ^{15}N). N_{mass}, the percentage of leaf mass that is nitrogen, is closely associated with maximum photosynthetic capacity of a leaf and thus is an important component of the leaf economic spectrum (Wright *et al*. 2004). The C:N ratio of a leaf is a chemical indicator of nutritional value of the leaf. It is assumed that carbon in excess of growth will be allocated to defence (Bryant, Chapin & Klein 1983). Delta ^{15}N describes the difference in concentration of ^{15}N relative to atmospheric levels and indicates a plant's utilization of different nitrogen pools (Spriggs, Stock & Dakora 2003). Concentration of ^{15}N is lower in atmospheric nitrogen than in soil organic nitrogen (Shearer & Kohl 1986). Thus, foliar delta ^{15}N is lowest (most negative) in plants associated with mychorrhizal fungi, where nitrogen comes from soil sources, and close to zero when the primary nitrogen source is from nitrogen-fixing bacteria (Spriggs, Stock & Dakora 2003; Hobbie & Hobbie 2008). We measured the chemical traits for eight native species and *E. umbellata*. It is noted that while these traits are often correlated with one another, the only significant correlation between traits we found was between N_{mass} and C:N ratio ($R = 0{\cdot}94$, $P < 0{\cdot}001$). Thus, with the aforementioned exception, we are dealing with largely independent trait dimensions in these analyses.

SAMPLING AND PROCESSING

We sampled a total of 2068 leaves from 209 plants representing one invasive and 11 species of native woody plants all growing in the understorey of the forest, and measuring between 1·00–3·18 cm dbh between June–August 2008 (Table 1). Branchlets were collected from each tree or shrub, brought to the laboratory for overnight rehydration and analysed the following day. Ten leaves were chosen from each sample, focusing on leaves with no epiphylls and little or no herbivore damage. Each leaf was scanned using a CanoScan 8800F and analysed using WinFolia 2005b (Régent 2005) to provide a suite of measurements of each leaf. Wet mass was measured for the leaf samples following scanning. After at least 72 h of drying at 60 °C, we measured leaf dry mass. We calculated LDMC as (leaf dry mass)/(leaf wet mass) and SLA as (leaf area)/(leaf dry mass). For chemical analyses, we bulked leaves from each individual and ground the samples to a fine powder with a ball mill. We analysed N_{mass}, C:N ratio and delta ^{15}N using a mass spectrometer. These analyses were run in an ecological chemistry laboratory at the University of Michigan.

ANALYSES

Trait overlap between native and invasive species

To answer our first question regarding an empty niche in trait space, we used a kernel calculator to estimate species trait distributions and overlaps (Mouillot *et al.* 2005). We calculated the overlap as the integral of the intersection area of the species trait kernel distribution when superimposed on a single trait axis. We compared the maximum, minimum and average pairwise overlaps by species. A communitywide mean overlap index was calculated by averaging the values of all native species pairs. For each trait, we also compared average species and community-based values with similar values of the overlap of *E. umbellata* with the native species and the overlap of *H. virginiana* with all other native species.

Trait distribution and rank order

To answer our second question regarding an expansion of community trait space, we calculated species means and standard deviations for each trait and ordered them along trait axes. Tukey HSD was used to determine which species differed significantly in which traits from *E. umbellata* and hence position it in trait space. Special attention was given to the comparison of *E. umbellata* and the native understorey shrub *H. virginiana*.

Results

TRAIT OVERLAP BETWEEN INVASIVE AND NATIVE SPECIES

Elaeagnus umbellata demonstrated the lowest pairwise overlap for four of the six traits observed (Table 2; Fig. 1). *Elaeagnus umbellata* overlapped less on average with the native species than the community average in five of six traits regardless of whether the invasive species was included in the community average (Table 2; Fig. 1). The difference in these overlaps is particularly substantial for all three chemical traits: leaf N_{mass}, C:N ratio and delta ^{15}N.

The native shrub, *H. virginiana*, overlapped similarly to the community average when compared only to native species and was among the highest average overlap for SLA and LA (Table 2; Fig. 1). For all traits, *H. virginiana* overlapped more with the entire community than *E. umbellata*. For all traits except log(SLA), *H. virginiana* had a higher maximum overlap with the rest of the community than *E. umbellata*, and for those traits, the pairwise overlap of *H. virginiana* and *E. umbellata* was below the community average and among the lowest overlap values for four of the six traits.

While it was not one of our *a priori* tests, we note the higher similarity in trait distributions of *Sassafras albidum* (Nutt.) Nees to *E. umbellata* for all traits except LA, where they are at opposite extremes (Figs 1 and 2). *Elaeagnus umbellata* shared a higher overlap value with *S. albidum* than *H. virginiana* with *S. albidum* for all traits except log(SLA).

TRAIT DISTRIBUTION AND RANK ORDER

Elaeagnus umbellata fell at the extreme end of trait space for LA, N_{mass}, C:N ratio and delta ^{15}N, and within one position of the extreme for LDMC (Fig. 2). *Elaeagnus umbellata* also had a high SLA, falling within the top three species. For four of the six traits considered, *E. umbellata* was significantly different ($P < 0{\cdot}05$) from all but *S. albidum* (Table S1). For SLA, *E. umbellata* was significantly different from all species apart from *Carya glabra* and *S. albidum*, and for LA, *E. umbellata* was statistically different from all species but *Prunus virginiana* L.

Hamamelis virginiana fell at the extreme low end of trait space for N_{mass}, at the opposite extreme to *E. umbellata*. It also represents the second highest mean trait value for C:N ratio and delta ^{15}N (Fig. 2). However, *H. virginiana* was only signifi-

Table 2. Summary of average pairwise overlaps by described assemblage and traits. In the latter two cases, we show the average pairwise overlap of a single species, either the invasive or native shrub, with all (other) native species

	Trait					
Assemblage	log(SLA)	N_{mass}	LDMC	C:N ratio	log (LA)	delta ^{15}N
All native	0·460	0·282	0·408	0·232	0·464	0·389
Invasive with natives	0·471	0·051	0·122	0·030	0·288	0·025
Native shrub with other natives	0·572	0·270	0·323	0·271	0·549	0·291

LA, leaf laminar area; LDMC, leaf dry matter content; SLA, specific leaf area.

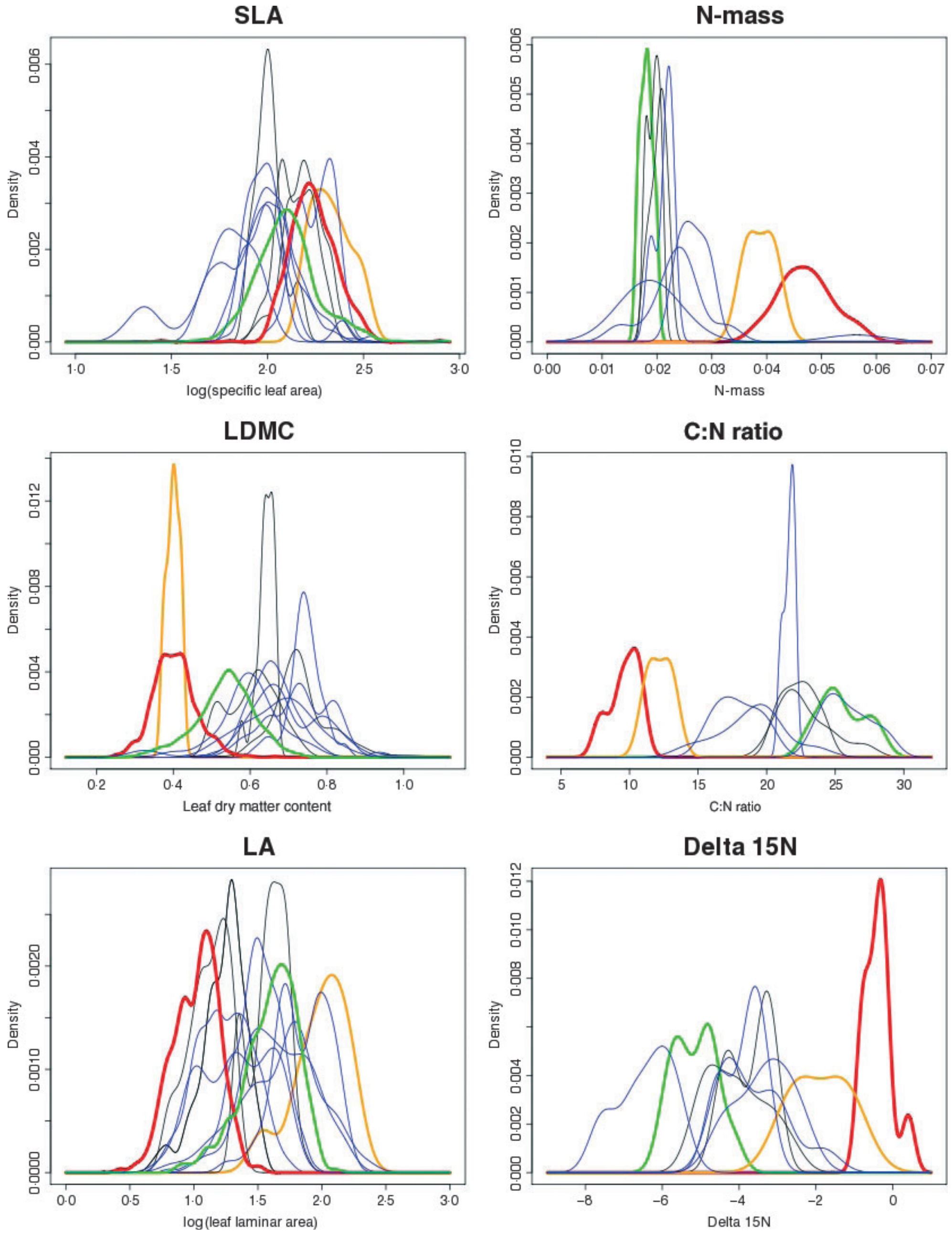

Fig. 1. Community trait axis constructed by the kernel density, shown as a proportion, (y-axis) of trait values (x-axis) for each species. Colour legend: *Elaeagnus umbellata*, red; *Hamamelis virginiana*, green; *Sassafras albidum*, gold; native canopy trees, navy blue; and native understorey trees, black. Note the similarity between *Elaeagnus* and *Sassafras* for many of these traits, and the dissimilarity between the two shrub species.

cantly different from two of the other nine species that were tested for N_{mass} and was statistically different from all of the other species except the extreme mean trait value represented by *Acer rubrum* L. for C:N ratio (Table S1).

Discussion

ECOLOGICAL STRATEGY IS NOVEL IN COMMUNITY AND MOST SIMILAR TO SUN-DEMANDING TREE

Results from this study support the empty niche hypothesis that posits invasive species will utilize resources, or in our case, demonstrate trait ranges that are distinct from those represented by the native community. For five of the six traits observed, *E. umbellata* has a lower maximum pairwise overlap and overlaps less on average with native species than the community average (Fig. 1). Furthermore, the values observed for these traits are consistent with the 'fast-return on investment' end of the leaf economic spectrum, including its associated defence and leaf chemistry traits (Wright *et al*. 2004). This suggests a sun-demanding species, especially in a resource limited forest habitat. This finding highlights the need for caution in applying the empty niche hypothesis to these traits; doing so would suggest that any sun-demanding species should invade

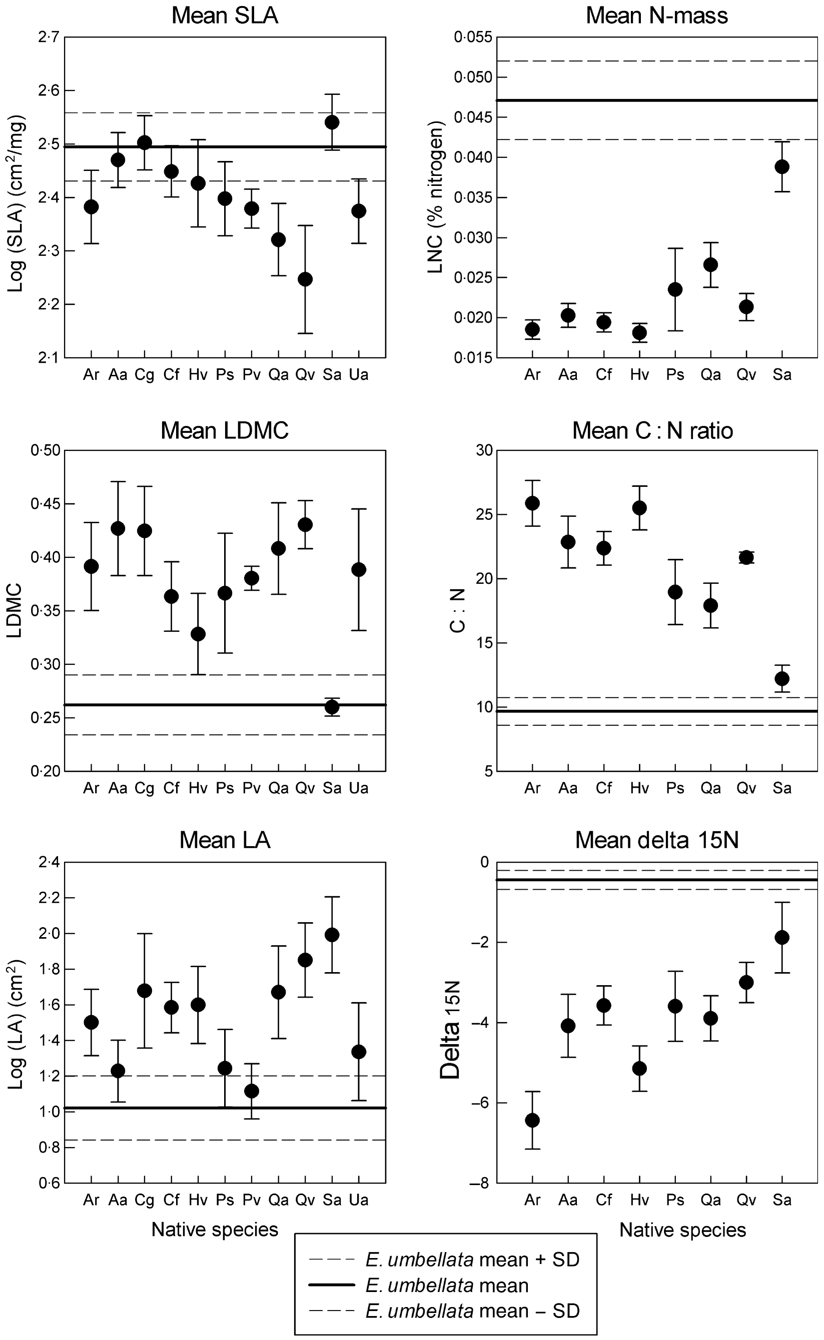

Fig. 2. Mean trait values with single standard deviation indicated by error bars by species. *Elaeagnus umbellata* is shown by reference lines. See Table 1 for abbreviations.

the understorey woody plant community, a prediction clearly not borne out in fact.

In addition to occupying distinct trait space from the native woody plant community, *E. umbellata* expands the trait space of this Michigan understorey community. In particular, we find *E. umbellata* expanding trait space in the direction characteristic of more sun-demanding plants. *Elaeagnus umbellata* exhibited the extreme trait value for LA, N_{mass}, C:N ratio and delta ^{15}N (Fig. 2). High SLA and N_{mass} values observed and low LA are consistent with a high photosynthetic capacity of *E. umbellata* leaves, indicative of a fast-growing, light-demanding gap species and a high potential for invasion (Wright *et al.* 2004; Grotkopp & Rejmánek 2007). In this case, the expansion of trait space is surprising given that higher light levels are not readily available in the understorey community following leaf out of canopy trees relatively early in the growing season. Existing trait ranges of native communities are seen as a reflection of niches readily available in the community. An expansion by an invasive, particularly in a surprising direction given knowledge of the community, suggests the invasion could be transitory or that some additional mechanism is at work enabling the invasive to use trait space not utilized by native species. Specifically, it seems that this species is finding a way to 'cheat' on established trade-off axes.

Considering functional similarity, we hypothesized that understorey shrub species occurring in similar environments would share similar trait-based ecological strategies. However, *H. virginiana*, the site's only native shrub, was more similar to the shade-tolerant trees of the native community than to *E. umbellata*; often these two shrubs occupied opposite ends of the trait spectrum. *Hamamelis virginiana* demonstrated most traits we would expect for a shade-tolerant species (low N_{mass}, high C:N ratio), while *E. umbellata* demonstrated characteristics of a sun-demanding species discussed earlier (e.g. Reich *et al.* 1998; Rozendaal, Hurtado & Poorter 2006). In spite of having a higher C:N ratio than the invasive species, substantial herbivory was noted for *H. virginiana* (Z.T. Brym, personal observation), suggesting its poor nutritional value did not prevent damage.

Surprisingly, we found that the invasive shrub is most similar in ecological strategy to a native sun-demanding tree, *S. albidum*. Trait means of *E. umbellata* were more similar to those of *S. albidum* than the remainder of the native community (Fig. 2). *Sassafras albidum* is closest in trait space to *E. umbellata* in five of six traits. Strikingly, while *E. umbellata* is well represented in the understorey, *S. albidum* is largely restricted to gap and edge habitat and is characterized as shade intolerant (Barnes & Wagner 2004). *Sassafras albidum* is not identified as allelopathic or a nitrogen fixer; these differences could help maintain *E. umbellata* in the understorey.

POTENTIAL MECHANISMS ALLOWING NOVEL TRAIT USAGE

Elaeagnus umbellata is expanding trait space in an unexpected direction for an understorey community, towards the characteristics of a sun-demanding species. Furthermore, its use of trait space is quite different from that of the native shrub species in the community. Instead, it demonstrates traits similar to that of a sun-demanding tree found only in gap and edge habitats. Given the strong demographic performance of the invasive species, transitory presence seems unlikely (Fig. S1). Thus, it seems that to compensate for limited light levels and truly establish in this community, *E. umbellata* must essentially 'cheat' on the typical trade-off associated with the leaf economic spectrum. We suggest that this relaxation of trade-offs could be facilitated through a release from natural enemies, association with nitrogen-fixing bacteria or efficient usage of a temporally available light resource. The low LDMC and low C:N ratio observed for *E. umbellata* indicate that its leaves would be quite palatable and nitrogen rich for herbivores. However, we did not observe the expected magnitude of herbivory (Brym, personal observation), and it is quite possible that enemy release has allowed it to maintain a positive carbon balance in shade, expanding its range beyond open canopy gaps (Dewalt, Denslow & Ickes 2004). It also appears that *E. umbellata* is using a different nitrogen pool from the native community, demonstrating the expected delta ^{15}N value (close to zero) related to bacterial fixation of atmospheric nitrogen (Shearer & Kohl 1986; Catling *et al.* 1997; Goldstein *et al.* 2010). Early-spring phenology (Miller-Rushing & Primack 2008) may also provide a temporally variable resource that allows for a seasonal advantage to the invasive species (Davis, Grime & Thompson 2000). *Elaeagnus umbellata* produces leaves and flowers earlier than the native woody plant species. Storing carbon earlier in the season may compensate for limited light availability for photosynthesis during the summer months.

Here, a limitation of a traits-based approach becomes apparent as our analyses must be supported with knowledge of the system to gain further understanding. Our demographic analysis suggests that *E. umbellata* is persisting, and even increasing, in a light environment that we would not expect following analysis of leaf traits. Additionally, our analysis fails to uncover distinct causal mechanisms for this observation. This may be due to factors that we observe through leaf traits, like release from herbivory or nitrogen-fixing capability. Through our understanding of the system, we further posited alternative mechanisms that were not directly explored within this study. Additionally, seeds of *E. umbellata* are broadly dispersed by birds, which tend to perch on branches in forested habitat (LaFleur, Rubega & Parent 2009). This means that vigorous individuals, with sufficient light in open grassland habitat, provide a large source of seeds to the understorey where the probability of successful recruitment increases with increased propagule pressure.

Conclusion

It is largely recognized that *E. umbellata* demonstrates a high propensity for invasion through prolific fruiting, rapid growth, high site adaptability and avian dispersal (Catling *et al.* 1997), but these and other traits of invasive species have not been previously considered in the context of the invaded community. Utilizing the traits observed, we show how an otherwise sun-demanding shrub might expand its range into understorey habitat. Nonetheless, simply considering the traits as measures of niche alone proved insufficient. By combining the trait data, an existing knowledge of the role of leaf traits in driving life-history strategies and growth rates, and census data on species occurrence, we were able to better understand how this species is interacting with the native understorey community.

The results of this study provide us with possible scenarios for the expected long-term community-level consequences of this invasion and allow us to consider the management implications. Transient presence can probably be excluded because the invasive population was increasing (Fig. S1). It seems likely that the presence of many small specimens represents advance regeneration; these shaded individuals survive the formation of a canopy gap and are then able to rapidly grow and reproduce (reviewed by Yamamoto 2000). While shade-intolerant species typically cannot survive in the understorey for long, it is clear that this invasive is managing to do so, despite shade-intolerant traits, at least in the medium term (5 years). However, it is not known whether this advance regeneration will lead to altered forest structure. In a worst-case scenario, it is possible that

E. umbellata will consistently outcompete all native species during early phases of gap regeneration, effectively leading to the replacement of forests with invasive shrub thickets. The invasive shrub severely limits light underneath its canopy (Brantley & Young 2009) and produces secondary chemicals that limit seedling germination and growth (Orr, Rudgers & Clay 2005). It further alters soil chemistry as a nitrogen fixer (Baer *et al.* 2006). Furthermore, as a bird-dispersed species, it is most probably being widely distributed throughout the forest, providing substantial source of propagules to understorey populations.

However, *E. umbellata* has two distinct disadvantages that may prevent its spread. First, it is likely that many, even most, of the native understorey species, which are more classically shade adapted, can establish and grow in the understorey just as well as or better than the shade-intolerant invasives. Second, almost all of these native species ultimately achieve a height greater than that of the invasives. Thus, to replace a forest, the invasive species would need to form large thickets that prevent advance regeneration of native species in an area sufficiently large to prevent shading from overtopping. It is not within the scope of this study to address the likelihood of these outcomes.

From a management perspective, ongoing elimination of these shrubs from the understorey could quickly become prohibitively expensive, as individuals will be small and scattered throughout the forest. Therefore, the current management strategy of limiting subpopulations in open habitat should be continued. This strategy not only will limit the negative impact on native grassland species but also has the benefit of decreasing propagule pressure arising from dispersal into forested habitats. Small seedlings are easily removed by hand pulling from moist soil, while large individuals are best controlled by cutting and a basal application of a generalized herbicide like triclopyr or glyphosate (Sather & Eckardt 1987). Concurrently, we suggest similar management approaches are adopted in recently formed gaps in forest to prevent recruitment or rapid growth of the invasive shrub during regeneration. This is likely where competition pressure from the invasive shrub will be most detrimental to native forest species. Assuming a worst-case scenario, management in understorey gap habitat would ensure the prevention of a fundamental shift in community composition.

Overall, this study demonstrates how trait-based approaches to community ecology can be used to better understand invasive species in the context of a native community. The results highlight the potential for this method to allow researchers to use relatively easily measured metrics to place potential invasive species onto trait and trade-off axes of local communities. It also, however, reveals that invasive species may be able to 'cheat' on these trade-offs through other unmeasured axes, and we caution that the use of traits alone may be misleading without the full context of the system's dynamics. It is also important to note that we selected traits focused on relatively few likely limiting resources in this community; it is important both to select traits appropriate to a given system and to recognize that it is impossible to measure all traits that may possibly be relevant. So long as the results of such studies are understood in the context of community dynamics and natural history, and trait axes are not viewed as direct surrogates of niche axes, these methods provide another tool in understanding invasive species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Relationship of relative growth in diameter and summed diameter of larger neighbours in 10 m radius of focal individual for *E. umbellata* and *H. virginiana.*

Table S1. Mean trait values and standard deviations.

Appendix S1. Demographic analysis of *Elaeagnus umbellata.*