

## Open minded and open access: introducing NeoBiota, a new peer-reviewed journal of biological invasions

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## Abstract

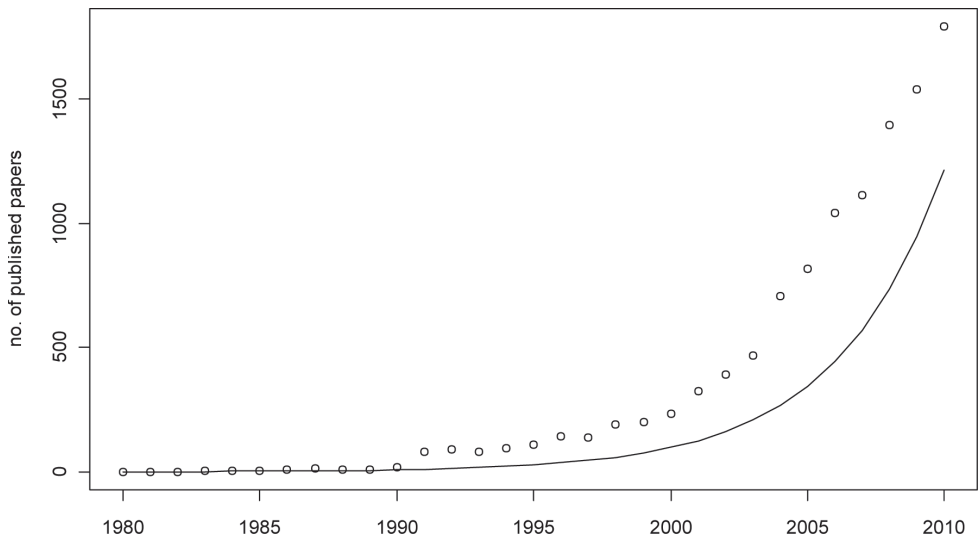
The Editorial presents the focus, scope, policies, and the inaugural issue of *NeoBiota*, a new open access peer-reviewed journal of biological invasions. The new journal *NeoBiota* is a continuation of the former *NEOBOTA* publication series. The journal will deal with all aspects of invasion biology and impose no restrictions on manuscript size neither on use of color. *NeoBiota* implies an XML-based editorial workflow and several cutting-edge innovations in publishing and dissemination, such as semantic markup of and enhancements to published texts, data publication, and extensive cross-linking within the journal and to external sources.

## Keywords

*NeoBiota*, invasion biology, alien species, semantic markup, semantic enhancements, data publishing

## Introduction

Introduced species have significant biodiversity impacts across all scales ranging from individual genes to global species declines that are shaped by a range of evolutionary, ecological, economic and societal mechanisms. As a consequence, biological invasions are a major challenge for current research, policy development and stakeholder response. International trade, transport and travel cause an ever faster increase in alien



**Figure 1.** The number of papers on alien or invasive species published per year (1980–2010) according to ISI Web of Science (accessed 1 July 2011, search string: topic=[alien plant\* or alien animal\* or alien species or biological invasions or plant invasions or animal invasions or “invasive species”]). The line indicates fitted exponential increase ( $R^2=0.96$ ,  $p<0.0001$ ).

species numbers (Hulme 2009; Pyšek et al. 2010; Chytrý et al. in press), while at the same time ‘invasion debts’ due to past socio-economic processes (Essl et al. 2011) provide ongoing and emerging challenges. Thus, research on alien species is a broad and innovative field of eminent importance from both theoretical and applied perspectives (Pyšek et al. 2006; Richardson and Pyšek 2008), and not surprisingly number of peer-reviewed papers published in the last 30 years has been rising exponentially (Fig. 1).

Despite much success in research on invasion biology, some scientists have claimed that this type of specialized research is uninformative and have suggested that it be integrated into more general ecological sub-disciplines (Marris 2009; Davis et al. 2011; Thompson and Davis 2011), which was vigorously opposed (e.g. Pyšek and Hulme 2009; Hulme et al. 2011; Simberloff et al. 2011; van Kleunen et al. 2011). Although the search for general patterns and mechanisms in ecology should be continued, this recommendation is oversimplified since biological invasions have become a general phenomenon in themselves shaping our views of evolutionary, molecular, restoration, population and community ecology (Simberloff and Rejmánek 2011). Of course, basic ecological patterns and processes are most likely similar for all species independent of their origin, but depending on the specific questions and geographic locations there are pronounced differences between native and alien species in their life-history traits (Crawley et al. 1996; Hovick et al. 2011), dispersion (Hulme 2008) and response to environmental drivers (Walther et al. 2009). While many alien species have negative ecological and economic impacts (Vilà et al. 2010), others may currently have no discernable effects

(Williamson 1996; Kenis et al. 2009; Kowarik 2010), and significant number of introduced species, mostly plants, have proved beneficial in the agricultural, horticultural and forestry sectors (Kühn and Klotz 2003; Lambdon et al. 2008). We can also expect that introduced species will continue to have an important role in the provision of food, fibre and fuel and contribute positively to ‘novel ecosystems’ that fulfil certain ecological functions in degraded habitats (Hobbs et al. 2006; Pyšek and Richardson 2010; Kowarik 2011), or in a changed climate (Walther et al. 2009). Thus, invasion biology has many important questions and promising areas that remain for future balanced analyses, and certainly it is a discipline too vigorous to die (Pyšek et al. 2008; Pyšek and Hulme 2009).

We therefore are confident that the field will thrive in the future. Some of the promising current and future topics we see are:

#### Mechanisms underlying biological invasions:

- How propagule pressure drives establishment success in different taxa and environmental circumstances.
- The impact on the invasion process of filters acting on individuals and species prior to them reaching novel environments.
- Quantification of dispersal mechanisms and vectors of introduction and spread.
- Traits that distinguish invasive alien species from non-invasive alien species and native species; relationship between species traits and invasion success.
- Importance of life history trade-offs along different stages of the invasion process.
- Demographic processes and the abiotic and biotic factors shaping them between native and introduced ranges of species.
- Relative importance of founding population size vs. genetic diversity in the establishment of new populations.
- Genetics and genomics of adaptation in invasive alien species.
- Climatic niche conservatism and the biogeography of invasive species.
- Effects of other global change components on biological invasions and interaction of invasions with such drivers, in first place climate change.
- Assembly rules and functioning of invaded biotic communities; mechanisms that allow alien species to coexist with native species.
- Mutualism or facilitation during the different steps of the invasion process.
- Invasiveness of understudied groups of organisms. Epidemiology of alien pathogens and parasites (e.g. fungi and micro-organisms).
- Comparisons of different ‘novel organisms’, especially alien species and genetically modified organisms.
- Quantifying the strength of biotic resistance to invasions among communities. Differences in invasibility of ecosystem types and their causes (e.g. disturbance, fragmentation).
- Harmonizing the different approaches that have been developed in different taxonomic groups into a common framework that allow true cross-taxon analyses of the factors driving the different steps of the invasion process (e.g. Blackburn et al. 2011).

Consequences of biological invasions at different scales:

- Post-invasion microevolution in native and alien species, including hybridization.
- Large-scale assessment of biodiversity changes at the gene and populations levels.
- Impacts on economy, human, plant and animal health; facilitation of human pathogens by alien species; ecosystem impacts ("changes in" biogeochemical cycles, flammability).
- Eco-evolutionary feedback between invasive traits and ecosystem function.
- Macroecological patterns of invasions at different scales and interaction among factors shaping them.
- Context dependence of invasion success and impacts.
- Impacts on endangered species and protected areas including long-term studies.

Assessing biological invasions:

- Taxonomic impediment and the need of correct identification of species.
- Standardization of collecting and storing data and of assessing invasion impacts to allow comparability across regions.
- Modelling tools to predict spatial spread of invasive species.
- Statistical techniques to account for biases and confounding factors; effects of data deficiency on the perception of factors associated with invasion success.
- Interface between scientifically backed analyses and value-based assessments of invasion consequences.
- Novel ecosystems and how to define and approach them.
- Ecosystem services and disservices
- Risk-assessment tools, developed for independent purposes at different scales.

Managing biological invasions:

- Social and political aspects of biological invasions.
- Control or management of introduction vectors to avoid further species to arrive.
- Ballast water management and compliance control technologies to assess whether standards were met.
- Rapid practical implementation of advances in invasion biology for prevention, eradication, and control of alien species.
- Restoration of invaded habitats and management of novel ecosystems.
- Risk analyses, black lists and other prevention tools.
- Legal measures and their implementation.

## Why 'NeoBiota'?

While the publication of Elton's (1958) book *The Ecology of Invasions by Animals and Plants* is often considered the pioneering milestone in modern invasion ecology (Ricciardi and Maclsaac 2008; Richardson and Pyšek 2008), the European tradition in re-

search on biological invasions is actually older and rooted in botanical studies from the beginning of the 19th century (see Trepl 1990; Kowarik and Starfinger 2009). However, European research on invasions, for example in Germany, was fragmented until the end of the 20th century with little cooperation between plant and animal ecologists and those working on terrestrial, freshwater and marine ecosystems, or on the pure and applied sciences (Kowarik and Starfinger 2009). To address this situation, a first meeting of invasion biologists was convened in Berlin in 1999 with the aim of integrating all aspects of invasion research, with the ultimate goal of reducing the threats to biological diversity. From this meeting arose an informal association of scientists, whose aims were: (i) to enhance communication and contact among scientists working on theoretical and applied aspects of biological invasions; (ii) to stimulate research on non-native species, their traits, distribution, related impacts and underlying mechanisms; (iii) to identify information deficits and co-ordinate efforts to fill them; and (iv) to disseminate information on causes, mechanisms and impacts of biological invasions, and on management approaches.

The resulting group was named 'NEOBIOTA', coined as an overarching term that would encompass all groups of organisms and avoid negative associations (Kowarik and Starfinger 2009). Terms such as 'invasion', 'alien' or 'exotic' were discounted as having negative connotations, since the group was interested not just in problematic non-native species, but also in species with neutral or beneficial impacts. Kowarik (2002) defined „*neobiota* as organisms, independent of their taxonomic rank, that occur in a region beyond their native range due to human agency or that evolved from such taxa". Hence, neobiota is an umbrella term for all non-native species without defining these by a negative or a value laden approach. Quite quickly, NEOBIOTA developed from a German to a Central-European and then pan-European working network with biennial conferences (see Kowarik and Starfinger 2009 for details). During the 6th NEOBIOTA conference in Copenhagen in 2010, the participants agreed on launching an international, peer-reviewed journal, named *NeoBiota*, and advocated for an open-access platform.

The new journal *NeoBiota* is a continuation of the former NEOBIOTA publication series, therefore it starts with No 9. Volumes 1–8 of NEOBIOTA can be seen at: <http://www.oekosys.tu-berlin.de/menue/neobiota>.

## Why a new journal?

In face of the eminent and increasing importance of biological invasions there is demand for a new journal that provides open access to a broad array of theoretical and applied invasion topics across all taxa and ecosystems. A further significant reason to launch a new journal is the need to respond to the major technological shift in academic publishing practices during last decade which will ensure important advantages for both authors and readers.

The new journal *NeoBiota* publishes papers without size limits across all disciplines dealing with biological invasions, encompassing the ecology, evolution and biogeogra-

phy of non-native aquatic and terrestrial animals, plants, fungi and microorganisms, on mechanisms that drive the introduction, establishment and spread of these species, on ecological, evolutionary, economic and other consequences of biological invasions, and on the management of invasions in any part of the world. No bias will be attached to the impact of non-native species, whether it is negative or positive, and all aspects related to a particular topic will be considered. *NeoBiota* therefore also strongly encourages papers on ethical, social, legal and policy issues related to biological invasions. *NeoBiota* considers the following categories of papers for publication: (i) original research articles, (ii) reviews as longer articles that offer a comprehensive overview, historical analysis or future perspectives of a topic, (iii) monographs and collections of papers on a specific topic with no limit in size, published as 'special issues', (iv) short communications, letters and discussion papers, and (v) book reviews.

The articles selected for the inaugural issue of *NeoBiota* largely reflect the vision of the editors of encouraging innovative and timely contributions to the new journal. The paper of Mack and Smith (2011), for example, addresses the increasingly important interface between biological invasions and human health by illustrating the role of invasive plants for spreading human parasites. The contribution by Moravcová et al. (2011) sheds light on interactions between introduced and native species by demonstrating potential phytotoxic effects of invasive *Fallopia* taxa, and Kowarik and von der Lippe (2011) disentangle, by using an experimental approach, the functioning of secondary wind dispersal in traffic corridors from that of other vectors. Finally, the contribution by Guo (2011) addresses, as a critical methodological challenge, how to count exotics at different spatial scales.

### **Why innovative and open access?**

The past decade has witnessed an unprecedented revolution in the way science is published and communicated. This revolution is driven by the Internet as a new media and communication environment and by open access publishing models (Suber 2010). Currently, we see the rapid move to the semantic Web (Web 2.0) and linked data environments (Berners-Lee et al. 2006), as well as an increasing strength of the open knowledge movement (see Open Knowledge/Data Definition and Panton Principles for Open Data in Science). The 'journals of the future' are meant mostly as various kinds of social networks, serving the interested community and reaching out to a wider audience, providing barrier-free, express and concise information, as well as access to underlying data. Content published in the journals of the next generation will be linked to various related sources and automatically distributed through community networks, wiki environment, indexing and aggregation services. An important trend with expected major impact on science communication is the 'atomization' of the content, that is dissemination both at the level of individual articles, as well as at the level of intrinsic parts of an article, such as taxon treatments, locality records, habitat descriptions, and others.

By having opted for open access and use of innovative publishing and dissemination methods applied in Pensoft's journals (see for more detail: Penev et al. 2009, 2010a, b, 2011), we intend to make *NeoBiota* a rapid means of communication with a quick editorial turnaround and time-to-publication process, as well as an efficient system of cross-linking of published content to external biodiversity and bibliographic platforms.

Thus, *NeoBiota* will respond to the present-day cultural and technological revolution in scholarly publishing and communication through:

- Open access to all scientific content published in the journal, with the barrier-free environment for the dissemination of scientific results, hence increased visibility and citation probability, that will benefit our authors and the scientific community in general.
- Strong support and provision of infrastructure for open data publishing, recognizing the crucial importance of up-to-date information on how to manage biological invasions, whilst facilitating the archiving, use and re-use of data, increasing the efficiency of data sampling-efforts, as well as the overall transparency and quality of the science.
- Development and implementation of various methods for semantic mark-up of and semantic enhancements to published texts, to ensure a pleasant and efficient reading process, as well as wide dissemination of separate parts of an logically 'atomised' article's content.
- Publication of identical content in four different formats to serve different target user groups: (1) full-colour, high-resolution print version; (2) PDF for reference to the printed version and easy archiving; (3) HTML for easy reading, browsing and applying semantic enhancements to the text; and (4) XML to provide a machine-readable file for archiving and data mining.
- Automated cross-linking through the Pensoft Taxon Profile with major indexing and aggregation platforms, such as the Global Biodiversity Information Facility (GBIF), Encyclopedia of Life (EOL), the International Plant Name Index (IPNI), ZooBank, the National Center for Biodiversity Information (NCBI), Genbank and Barcode of Life, the Biodiversity Heritage Library (BHL), PubMed, PubMedCentral, Mendeley and many others.
- Increased public awareness of scientific results on biological invasions through an already established system of press releases associated with published articles, science and general blogs, social networks and others.

With these new techniques and novel publishing methods backing up *NeoBiota*, we are confident we will contribute successfully to facilitating research and education on invasion biology and to the swift communication of scientific results. By joining forces with an innovative and ambitious publisher we aim to make the science on biological invasions more open, efficient and of great benefit to scientists, research funders and society in general.



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# Invasive plants as catalysts for the spread of human parasites

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## Abstract

To a degree not widely recognized, some naturalized and invasive plants increase the risks to human health by enhancing the proliferation of vectors of virulent human parasites. These potential risks are restricted by neither ecosystem nor geography. The dense, floating mats of the tropical South American invasive macrophyte *Eichhornia crassipes* (water hyacinth) creates habitat for larvae of the dipteran vectors of *Plasmodium* spp., the causative agents of malaria, and other parasites. In Africa, the South American shrub *Lantana camara* (lantana) provides suitable habitat in otherwise treeless areas for dipteran vectors (*Glossina* spp.) of protozoans (*Trypanosoma* spp.) that cause trypanosomiasis. In the eastern United States, proliferation of the invasive *Berberis thunbergii* provides questing sites for the blacklegged ticks that carry the spirochete *Borrelia burgdorferi*, the causative agent of Lyme disease. Unanticipated health consequences will likely continue to emerge from new plant introductions. Hantaviruses are rodent-borne parasites that cause lethal hemorrhagic fevers in humans. Populations of rodent Hantavirus vectors in South America increase rapidly in response to fruit availability among masting, native bamboos. In the United States the omnivorous deer mouse *Peromyscus maniculatus* also carries Hantavirus (Sin Nombre Virus). The on-going escape of Asian frost-tolerant bamboos from cultivation raises the possibility of their becoming invaders - several have already become naturalized - and in turn providing a temporary food source for populations of infected native rodents. Proposed introductions of floating aquatic vascular species, species with masting reproduction and species that could occupy an unfilled niche in a new range deserve careful evaluation as catalysts of unintended species interactions, especially of human parasites.

## Keywords

bamboos, disease, hantavirus, malaria, quarantine, schistosomiasis, trypanosomiasis, vectors

## Introduction

Deliberate plant introductions often produce unexpected, but decidedly negative, consequences in their new range. Most attention is directed currently at immigrant species that become naturalized or even invasive (*sensu* Mack et al. 2000), i.e., exerting effect over a new range by usurping the role of native plants (or valued non-native species) through competition (Flory and Clay 2010), altering the water or fire regime (D'Antonio 2000), impeding navigation (Gopal 1987) or disrupting mutualisms (Richardson et al. 2000). These consequences can have simultaneously a strong economic as well as environmental component (Pimentel et al. 2000; Pimentel 2002).

Examples in which the introduced species jeopardizes the health of vertebrates, including humans (Burrows and Tyre 2001), form a category of naturalizations/invasions that are viewed with special concern. These species can act by either causing severe contact dermatitis (*Heracleum mantegazzianum*, Pyšek et al. 2007) or debilitating respiratory trauma (*Parthenium hysterophorus*, Parsons and Cuthbertson 1992), or the production of toxins that are fatal if ingested (*Bryonia alba*, *Datura stramonium*, *Nerium oleander*) (Turner and Szczawinski 1991). Much deserved attention has been directed at identifying, prohibiting the transport, and controlling outbreaks of poisonous plants in new ranges (e.g. Plant Protection Act, USDA 2000). Consequently, the risk of new introductions of toxin-producing species has fallen (Westbrooks 1981).

We propose here a further, largely unrecognized, category of persistent introduced plants for which their negative consequences had not been foreseen: those that serve as indirect catalysts for the transmission of human parasites. In these cases, far from bringing about a perceived beneficial effect (e.g. fuel, food, forage, medicine), the introduced plants exacerbate the incidence of human suffering. Our initial examples involve previously reported interactions of introduced plants, vectors and parasites. In our final example, we contend that the current introduction of leptomorphic bamboos could increase the incidence of a highly lethal disease (Hantavirus Pulmonary Syndrome) in North America and elsewhere.

## Introduced aquatic macrophytes: facilitation by *Eichhornia crassipes* of the dipteran and snail vectors of human parasites

Water hyacinth (*E. crassipes*) (Pontederiaceae) is a widely introduced macrophyte that is a serial invader in the tropics and subtropics and is even naturalized at temperate latitudes (Holm et al. 1977, Gopal 1987, Barrett 1989). *E. crassipes* is often termed “one of the world’s worst weeds” (Holm et al. 1977) or even “the world’s worst weed” (Cook 1990) – epithets that invoke sizeable biome bias, as the plant requires freshwater environments above 5°C (Owens and Madsen 1995). Nevertheless, the damage it inflicts can be undeniably massive to aquatic communities and humans dependent on these freshwater ecosystems for food, transportation (Gopal 1987) and potable water (Mailu 2001).

The invasion by water hyacinth of communities fringing Lake Victoria and its connected rivers best illustrate the damage this plant has wrought. From its early detection in Lake Victoria in 1989 (Twongo 1993), the invader spread mainly through the production of ramets around the lakeshore; it occupied as much as 80% of the shoreline in Uganda alone (Mailu 2001). At the maximum measured extent of *E. crassipes* in 1998, it had occupied more than 17,000 h and likely much more (Albright et al. 2004). Julien (2008) estimates that under ideal growing conditions (and assuming unlimited ability for the population to spread radially) an initial two kg of water hyacinth could produce 16 tonnes of plant material after six months!

As part of a litany of environmental/economic costs, water hyacinth facilitates the incidence of human disease by increasing the habitat for aquatic dipterans, particularly those anopheline mosquitoes that carry the causative agents for malaria (*Plasmodium* spp.). A link between water hyacinth and the incidence of malaria has been recognized for decades (e.g. Barber and Hayne 1925, Meyer 1947, Gopal 1987 and references therein), although the clear experimental evidence, e.g., side-by-side trials with water hyacinth and native lakeshore vegetation, has apparently yet to be performed. The stagnation or reduction in water current by large mats of water hyacinth appears key here, by allowing *Anopheles* females to lay eggs (Merritt et al. 1992). The growth habit of *E. crassipes* with its short stolons and dense concentrations of ramets, long petioles, and a fibrous root system substantially impedes water current along a shoreline. Unlike its congener, *Eichhornia azurea*, water hyacinth can grow rapidly without roots attached to the underlying sediment (Barrett 1989). Although the protozoans that cause malaria resided in the Lake Victoria watershed long before the early 20<sup>th</sup> century arrival of water hyacinth (Clyde 1967), water hyacinth has increased the incidence of these parasites by greatly increasing habitat for *Anopheles* spp. (Gopal 1987, Feikin et al. 2010). Furthermore, the concentration of people living alongside a body of freshwater exacerbates disease incidence by providing a large group of susceptible hosts (Morse 1995) (Fig. 1).

Tragically, the habitat created by water hyacinth not only facilitates anopheline mosquitoes but can also create habitat for snails in the genera *Biomphalaria* and *Bulinus*, hosts for the flukes that cause schistosomiasis (bilharzia), and dipteran vectors (e.g. *Mansonia* spp.), of the nematodes that cause filariasis. The snails derive resting sites as well as food (algae and detritus) within mats of water hyacinth (Mitchell 1974). Ofulla et al. (2010) found that the vectors *Biomphalaria sudanica* and *Bulinus africanus* were preferably attached to *E. crassipes* in Lake Victoria, even becoming attached to water hyacinth in greater numbers than to the native hippo grass (probably *Vossia cuspidata*).

Adults of several *Mansonia* spp. infect humans with the nematode *Brugia malayi*, the causative agent of lymphatic filariasis (Roberts and Janovy 2009). The association of *Mansonia* spp. and water hyacinth in Southeast Asia is particularly extensive: all stages in the mosquito's development rely on the plant. Egg masses are commonly laid on the plant's young semi-submerged leaves. Later the larvae and pupae of *M. uniformis*, for example, swim to the plant's roots and become tightly attached to the fibrous roots (Burton 1960). The larvae must attach their siphons to *E. crassipes* to acquire O<sub>2</sub> (Chandra et al. 2006).



**Figure 1.** *Eichhornia crassipes* (water hyacinth) is widely distributed in waterways in the tropics and subtropics. The ability of its mass of fibrous, free-floating roots and semi-submerged leaves and stems to decrease water current increases habitat for anopheline mosquitoes, vectors for *Plasmodium* spp. As a result, its close association with human settlements often leads to an increase in vector-borne diseases, including malaria. Mekong River, at Viet Nam-Cambodia border. (Photo: RN Mack).

Water hyacinth has also been implicated in harboring the causative agent for cholera, *Vibrio cholerae*. Feikin et al. (2010) found a direct correlation from 1994–2008 in the incidence of reported cases of cholera in Nyanza Province, Kenya, which borders Lake Victoria, and the extent of the adjacent lakeshore occupied by *E. crassipes*. Two surges in the number of cases of cholera in Nyanza Province coincide with two pulses in the abundance of water hyacinth (1997–2000 and 2006–2008) - significantly more infections per capita than in Kenya as a whole. As they point out, correlation does not however demonstrate causation, especially as other factors could confound the results, including the incomplete reporting of cholera cases. They hypothesize that water hyacinth, rather than serving as a refuge for *V. cholerae*-carrying copepods, may instead provide a direct nidus for the bacterium, especially in its fibrous roots - a contention supported by experimental evidence (Spira et al. 1981). Alternatively, a shoreline packed with *E. crassipes* may concentrate contaminated sewage close to shore, thereby increasing the opportunity for infection, regardless of the bacterium's direct attachment to water hyacinth (Rejmánková et al. 2006).

Attempts to combat water hyacinth in new ranges have been waged for more than a century. Specific legislation authorizing the dredging or poisoning of water hyacinth



in Florida was enacted by the U.S. Congress in the late 1890s – to no avail (Klorer 1909). The identification and release of biological control agents (the weevils, *Neochetina bruchi* and *Neochetina eichhorniae*) in Lake Victoria from 1995 onward had successfully reduced the extent of water hyacinth mats by 2000 (Wilson et al. 2007). Nevertheless Julien (2008, p. 477) presents a grim view of the ability to remove a large infestation of water hyacinth, “Once it is established, it is impossible to eradicate,” although he views its integrated management as feasible. In short, the damage that water hyacinth inflicts, including its facilitation of the vectors of lethal parasites, shows few signs of abating.

### ***Lantana camara* harbors *Glossina* spp., vectors for trypanosomes**

Plant invaders that facilitate the spread of human parasites are not, of course, restricted to aquatic environments. If *E. crassipes* is touted as one of the worst invaders in freshwater ecosystems, then *Lantana camara* (Verbenaceae) must be among its most notorious counterparts on land. This tall shrub ( $\leq 5$  m tall) is native to tropical America, although its origins and phylogeny have only recently been clarified (Sanders 2006). *L. camara* refers to a multi-taxon hybrid swarm created by horticulturists, beginning in the 18<sup>th</sup> century, augmented by hybridizations within introduced ranges (Stirton 1977, Sanders 2006). Thus, *L. camara* is in effect the misbegotten product of the desire to create an ever more attractive ornamental plant. Sanders (2006) proposes the cultivars be re-named *L. strigocamara*. To avoid confusion in citing the epidemiological literature below, we refer here to the cultivar as *L. camara*.

So attractive and varied are the flowers of *L. camara* that the shrub has been spread and subsequently widely naturalized throughout the tropics and subtropics and can be cultivated even in some temperate locales (e.g. Auckland, New Zealand, RN Mack, personal observation). It is routinely one of the first introduced species encountered upon arriving in many tropical towns and villages, testimony in part to its abundant production of bird-dispersed drupes (Binggeli 2003). The zeal and intensity of its deliberate spread are perhaps best illustrated by the number of remote Pacific islands to which it has been introduced and has become invasive (e.g. Tonga, Pitcairn and Norfolk) (Thaman 1974).

Its link to human disease in Africa, for example, is attributable to its aggressive growth: it forms an impenetrable thicket of sprawling, intertwined (and often spiny) stems on disturbed or otherwise open sites. These thickets provide habitat for *Glossina* spp. (the tsetse fly), which are carriers of trypanosomes, such as *Tripanosoma brucei gambiense*; these protozoans cause African trypanosomiasis or African Sleeping Sickness. The World health Organization (WHO 2010) states best the consequences of protracted illness from African trypanosomiasis: “Without treatment, sleeping sickness is considered fatal.”

*Lantana* provides resting sites for adult *Glossina* flies in addition to sites for larviposition by *Glossina* spp. (Ng’ayo et al. 2005) either on the abaxial surface of leaves or

along small twigs in the intertwining mass of branches. The flies reside principally on the plant < 4 m above the soil surface (Okoth and Kapaata 1987). Unlike anopheline mosquitoes that search for a blood meal at night, *Glossina* is active in the day but must seek shade when the temperature > 40°C (Hargrove 1994). A wide, open site, such as a cleared forest or savanna, prevents *Glossina* dispersal (Nash 1969). The planting of lantana hedges to demarcate fields and property boundaries insidiously led to an increase in the incidence of African Sleeping Sickness in Kenya (Van den Berghe as cited in Nash 1969).

The association between *Glossina* and *L. camara* is facilitated by the shrub's production of volatiles. Syed and Guerin (2004) showed strong attraction by three *Glossina* spp. to lantana leaves and lantana leaf extract in wind tunnel trials. They then combined plant product chemistry with investigation of the flies' antennae receptors to identify an aromatic cocktail of two natural plant products most likely responsible for lantana's attraction: 1-octen-3-ol (or octenol), a secondary alcohol that is also produced in human sweat and attracts biting mosquitoes (Ditzen et al. 2008), and  $\beta$ -caryophyllene, a sesquiterpene that occurs as an active ingredient in many plants, including black pepper, cinnamon and oregano (Gertsch et al. 2008). These results are intriguing, although the efficacy of lantana as an attractant needs evaluation in the context of surrounding vegetation that could produce a vast array of competing chemical stimuli for dipterans.

Tragically, human conflict has repeatedly triggered the spread of the *Lantana-Glossina*-trypanosome assemblage in Africa, as refugees abandon their land and "bush clearing" is suspended in the war zone. In this manner the continual social upheaval during the regime of Idi Amin in Uganda during the 1970s led to an increased incidence of trypanosomiasis (in this case caused by *T. b. rhodesiense*) (Molyneux 1997). More recent human conflicts in the eastern Congo-Rwanda-Burundi region as well as in West Africa (e.g. Sierra Leone) have sadly created similar opportunities for the proliferation of lantana and consequently for *Glossina* (Reyntjens 2009).

Even during peacetime, the cultivation of *L. camara* in human settlements can facilitate disease in treeless areas with African Sleeping Sickness. A non-decorative use of lantana in Kenya has been the replacement of native euphorbs with spiny lantana hedges around cattle pens and to demarcate property boundaries; the result was an increase in the incidence of trypanosomiasis (Greathead 1968, Van den Berghe as cited in Nash 1969). The beauty of this perennially flowering shrub can be deadly with local people in East Africa planting – or at least not clearing – it around their rural homes (Okoth 1986). In effect, the human hosts are unknowingly cultivating resting sites for the tsetse fly alongside their dwellings (Willett 1965) – an insidious link between humans' universal desire for decoration (Mack 2001 and references therein) and their susceptibility to a deadly parasite. Furthermore, as cleared forest sites or crop fields have been abandoned, for whatever reason, in West and East Africa, *L. camara* has been among the most aggressive colonizers and has consequently created low stature shade, which is ideal for *Glossina* (Baldry 1966). Consequently, recommending the cessation

of lantana bush-clearing programs because the shrub can be a local source of firewood (Okoth and Kapaata 1987) is misguided at best and grossly negligent at worse.

### ***Berberis thunbergii* alters eastern North American forests and increases habitat for Lyme disease vector, *Ixodus scapularis***

Not surprisingly, facilitation of the spread of human parasites by invasive plants is not restricted to tropical locales. Among the best-studied examples in temperate environments involves the contraction of Lyme disease, a debilitating inflammatory condition caused by the tick-borne spirochete, *Borrelia burgdorferi*. Links between invasive shrubs (principally *Berberis thunbergii* but also non-native *Lonicera* spp., Lubelczyk et al. 2004), the blacklegged tick (*Ixodus scapularis*), *B. burgdorferi* and most importantly the white-tailed deer as well as other mammals, such as the white-footed mouse (*Peromyscus leucopus*), have been the subject of ecologically comprehensive research (Ostfeld et al. 2006, Williams et al. 2009, Williams and Ward 2010).

Non-native *Berberis* and *Lonicera* were introduced pre-1900 to North America as horticultural ornamentals (Mack 1991) and have subsequently spread into forests in the Eastern U.S., often through bird dispersal (Silander and Klepeis 1999 and references therein). Increase in the likelihood of the shrubs' persistence as well as their role outside cultivation has been furthered by their general unpalatability (Silander and Klepeis 1999) or greater resilience to grazing (Schierenbeck et al. 1994), compared to native understory competitors. As the coverage of these medium height shrubs (< 2 m) has increased in forests, so has the incidence of blacklegged ticks, for which the shrubs provide questing sites and maintenance of the high (approximately 90%) relative humidity, which is conducive to tick survival (Williams and Ward 2010 and references therein). In turn, as the density of deer populations has increased, so has the number of ticks that have become attached to them as they travel through the forests. Tick-laden deer potentially form a diabolical dual role in Lyme disease ecology: continually expanding and re-infecting the forest area harboring *B. burgdorferi* through their wide-ranging movements and selective grazing.

### **An ominous new threat: rodent-borne parasites facilitated by naturalized bamboos**

The examples provided above all describe on going, if under-appreciated, cases of plant invaders indirectly enhancing the incidence of human disease. Our attention has been drawn recently to the looming opportunity for a morphologically distinct group of plants, leptomorphic (or running, *sensu* McClure 1966) bamboos, to be transported to new ranges, and potentially trigger increases in the size of populations of *Peromyscus maniculatus* (deer mice), a native North American rodent.

Bamboos are unique among grasses in displaying synchronized flowering (i.e. masts), in which all individuals of a species flower within the same time frame (months to several consecutive years) worldwide and then die (Janzen 1976). The rapid appearance of abundant bamboo seeds can translate into the increase, however temporarily, of populations of seed predators. For example, a population of *Rattus rattus* can readily gorge on a bamboo seed crop and undergo rapid population increase. After exhausting this temporary food source, the rats disperse in search of food, often coming in contact with humans (Janzen 1976). Outbreaks of rats, sparked by masting bamboos, are well known in rural Asia and South America, and people living in these affected regions subsequently endure a sharp rise in the incidence of infections from rat-borne parasites (Jaksic and Lima 2003, Lalnunmawia et al. 2005).

Growing interest in ornamental bamboos for horticulture in the U.S. has facilitated the introduction of non-native species (American Bamboo Society 2010), including those with pronounced mast flowering cycles (Janzen 1976). Several of these species are now naturalized in the U.S. (USDA 2010) and consequently have already fulfilled the first critical demographic step on the path to becoming invasive. We hypothesized that synchronous flowering/fruitleting of a large population of invasive bamboo could initiate a rapid build-up in rodent populations with accompanying increases in parasite transmission, provided the rodents harboring the causative organism feed upon this novel food.

The deer mouse is an omnivorous (e.g. arthropods, seeds, fungi), widespread native rodent in North America and carries multiple human pathogens, including Sin Nombre Virus (SNV), *Francisella tularensis* (tularemia), *Yersinia pestis* (plague) and *B. burgdorferi* (Mills and Childs 1998, Netski et al. 1999, Feldman et al. 2001). Incidence of these diseases rises with increases in rodent populations (Yates et al. 2002). SNV is an especially serious health threat in Western North America: it causes Hantavirus Pulmonary Syndrome (HPS), a frequently fatal hemorrhagic fever (~35% mortality rate) (Netski et al. 1999). In this region, humans can readily encounter an infected deer mouse: e.g. 15% of deer mice trapped in Montana and Washington carry the virus (Pearson and Callaway 2006, Washington State Department of Health 2010), and deer mice often inhabit peridomestic structures (e.g. barns, sheds, granaries) (Douglass et al. 2006). Transmission of SNV to humans occurs primarily through contact with or inhalation of aerosolized urine and feces (Netski et al. 1999).

We evaluated the ability of *P. maniculatus* to survive and reproduce solely on a diet of Asian bamboo (*Bambusa distegia*) fruits in laboratory feeding trials in comparison to diets of laboratory rat chow and the seeds of two native species, *Pinus ponderosa* and *Festuca idahoensis*. Females fed bamboo seeds reared significantly more pups than those fed lab chow and pine seeds (LS Mean pairwise comparison,  $P = 0.016$  and  $P = 0.042$  respectively). We observed no significant differences in weight per pup at weaning (ANOVA,  $F_{3,18}=2.06$ ,  $P = 0.1419$ ). With their short and prolific reproductive cycles, *P. maniculatus* populations could be particularly responsive to a suddenly available food, such as bamboo seeds (Gashwiler 1979).

Our predictions here deal only with the potential for large-scale spread of leptomorphic bamboos with aggressively spreading rhizomes. Coniferous forests along the

west coast of North America and inland, in which *P. maniculatus* is common and locally prominent (Converse et al. 2006), may be particularly at risk of invasion by frost-tolerant bamboos, given the strong climatic similarity of these bamboos' native range in temperate Asia and the northwest coast of North America. Use of ornamental running bamboos in landscaping is increasing in the region, both in its popularity and in the number of introduced species (American Bamboo Society 2010). An opportunity for these species to become naturalized in North America appears probable. For example, *Sasa kurilensis*, a dwarf (< 2 m) running bamboo forms a continuous hedge-like layer in Asian coniferous forests that bear many floristic and physiognomic similarities to forests in western North America (Numata 1979, Tsuyuzaki and Kanda 1996) (Fig. 2).

Running bamboo species could greatly increase the numbers of rodents first by providing concealment from predators for them in the forest understory and ultimately by providing abundant food. In a worst-case scenario, a naturalized bamboo population undergoes mass flowering/fruitletting on remote public lands, resident *P. maniculatus* populations rapidly increase, driven by the newly available resource, to be followed by bamboo eventually waning as a food source. As a consequence, starving peridomestic *P. maniculatus* disperse into adjacent human settlements. The well-known difficulty of removing bamboos, given their extensive rhizome and root systems (Whittaker 2005), amplifies the potential seriousness of this public health issue.

### **Future threats of plant invaders as catalysts for the spread of human parasites**

The opportunity for the inadvertent creation of new plant invasions continues, given our frequent inability to predict the invasive potential of species, other than a growing list of "usual suspects", i.e., those species already banned for importation, based on their record as pests. Assessment of new invaders is daunting (National Research Council 2002): not only is accurately predicting a species' performance in a new range challenging, but any regulatory decision arising from a prediction needs to provide phytosanitary protection without forming a constraint to free trade (Mack et al. 2000). A comprehensive assessment of this topic is beyond the scope of our paper. However, we suggest some general plant functional groups or life forms that merit increased scrutiny as potential catalysts for the spread of human parasites.

*Aquatic vascular plants.* This category comes as no surprise, given the link between water hyacinth and human disease. As land is flooded through impoundment downstream, a new shoreline is effectively created. Aquatic species already within the watershed are readily transported into the new body of water. Such dispersal has sometimes triggered a rise in the incidence of human disease, e.g. an outbreak of schistosomiasis associated with an invasion of *Pistia stratiotes* and *Ceratophyllum demersum* in Lake Volta in Ghana in the 1960s (Paperna 1970). Creation of a new lake may not however immediately lead to an invasion of alien aquatic species (Bond and Roberts 1978). But the potential strongly suggests that early incursions of these species should be care-



**Figure 2.** Leptomorphic or running bamboos (e.g. *Sasa kurilensis*) form prominent swards in the understory of coniferous forests in temperate eastern Asia. As masting species bamboos periodically provide a large, if temporary, food source for rodents that carry human parasites. Depletion of the food commonly drives the rodents into human contact with concomitant rises in human disease. Introduced leptomorphic bamboos could produce similar consequences in North America for *Peromyscus maniculatus*, a vector of the lethal Sin Nombre Virus (SNV). Daisetsuzan National Park, Japan. (Photo: RN Mack).

fully surveyed for negative consequences, if their entry and establishment cannot be prohibited.

*Masting species.* Bamboos are not the only plants with synchronous reproduction. Masting occurs in many boreal forest conifers (Koenig and Knops 2000) and tropical trees (Sork 1993). Despite the radically different physical environments in which conifers and tropical trees occur, masting has arisen in many woody species; explanations vary but seed satiation remains a likely outcome in many cases (Kelly 1994). Oaks also display masting and provide a well-investigated example of the linkage between seed production and human disease. As noted above, hosts for the blacklegged ticks that carry the causative agent of Lyme disease in the eastern U.S. include the white-footed mouse, *P. leucopus*. Sizes of these omnivorous rodents' populations rise when acorns are abundant, increasing in turn the density of ticks and eventually the incidence of Lyme disease in humans (Jones et al. 1998). We urge caution (and post-immigration

field evaluation, Davis et al. 2010) in the introduction of any masting species into a new range.

*Absent life forms.* Non-native species filling this role form the most taxonomically and morphologically diverse of the categories we believe deserve heightened attention by quarantine services. Many, but by no means most, plant invaders attain their new role by filling a niche unoccupied by a native species (or occupied by a weak native competitor). Examples abound, from the invasion of the European grass *Spartina anglica* on tidal mud flats along the West Coast of North America to the massive transformation of the Everglades marsh in Florida by the Australian tree, *Melaleuca quinquenervia* (Mack 2003). Establishment of a novel life form (*sensu* Raunkjær 1934) invariably creates novel interactions with the native and non-native species, as well as creating opportunities for other immigrant species previously unable to reside in the new range.

The paucity in the native tropical East African flora of large, floating macrophytes that form mats may explain in part the devastating invasion of *E. crassipes* into so many African waterways. For example, the native flora contains only three species within the Pontederiaceae, *Eichhornia natans*, *Heteranthera callifolia*, and *Monochoria africana* (Verdcourt 1968); none of these species display the unusual morphology of *E. crassipes*, which is so conducive to forming inter-tangled mats (Barrett 1989). About half a dozen native taxa occur in the East African Nymphaeaceae, another plant family with species that produce floating leaves (Heywood et al. 2007). But here again, none has the growth form that produces an ideal habitat for dipterans (Verdcourt 1989). The question remains of course, whether other aquatic vascular plants, yet to be introduced to East Africa, or other regions with few native macrophytes could duplicate the role now occupied so tenaciously by water hyacinth

### **Need for further collaboration among epidemiologists, ecologists and quarantine services**

We call attention here to a largely overlooked – or at least inadequately appreciated – link between invasive plants and the incidence of human disease. Exhaustive examination of the biology of human parasites, their vectors and other modes of dispersal and transmission has long been a pillar of field epidemiology worldwide (Simmons et al. 1944, Gregg 2002, Rothman et al. 2008). Consequently, it would be inaccurate to claim that the broader ecological context of disease transmission has been ignored. Instead we alert epidemiologists and ecologists to another category in which their investigations warrant substantial and productive overlap – the search for (and prevention of) new examples in which an immigrant plant species arrives by whatever means in a new range and sparks an increase in human disease and its attendant, preventable suffering.

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# Potential phytotoxic and shading effects of invasive *Fallopia* (Polygonaceae) taxa on the germination of dominant native species

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## Abstract

Two species of the genus *Fallopia* (*F. sachalinensis*, *F. japonica*, Polygonaceae) native to Asia, and their hybrid (*F. ×bohemica*), belong to the most noxious plant invaders in Europe. They impact highly on invaded plant communities, resulting in extremely poor native species richness. The low number of native species in invaded communities points to the possible existence of mechanisms suppressing their germination. In this study we assessed, under laboratory conditions, whether there are phytotoxic effects of the three *Fallopia* congeners on seed germination of three target species: two native species commonly growing in habitats that are often invaded by *Fallopia* taxa (*Urtica dioica*, *Calamagrostis epigejos*), and *Lepidium sativum*, a species commonly used in allelopathic bioassays as a control. Since *Fallopia* taxa form dense stands with high cover, we included varying light conditions as an additional factor, to simulate the effects of shading by leaf canopy on germination. The effects of aqueous extracts (2.5%, 5.0%, and 0% as a control) from dry leaves and rhizomes of the *Fallopia* congeners on germination of the target species were thus studied under two light regimes, simulating full daylight (white light) and light filtered through canopy (green light), and in dark as a control regime. Rhizome extracts did not affect germination. Light treatments yielded inconclusive results, indicating that poor germination and establishment of species in invaded stands is unlikely to be caused by shading alone. However, we found a pronounced phytotoxic effect of leaf extracts of *Fallopia* taxa, more so at 5.0% than 2.5% extract concentration. *Fallopia sachalinensis*

exerted the largest negative effect on the germination of *Urtica dioica*, *F. ×bohemica* on that of *C. epigejos*, and *F. japonica* had invariably the lowest inhibitory effect on all test species. The weak phytotoxic effect of *F. japonica* corresponds to the results of previous studies that found this species to be generally a weaker competitor than its two congeners. Although these results do not necessarily provide direct evidence for allelopathic effects in the field, we demonstrate the potential phytotoxic effect of invasive *Fallopia* taxa on the germination of native species. This suggests that allelopathy may play a role in the impact of *Fallopia* invasion on species diversity of invaded communities.

### Keywords

Allelopathy, canopy shading, leaf and rhizome extracts, light regimes, phytotoxicity, plant invasions, *Reynoutria*

## Introduction

Recent research on biological invasions increasingly focuses on different types of impacts of invasive species (Levine et al. 2003; Vilà et al. 2010; Pyšek and Richardson 2010), amongst which the impact on the biological diversity of invaded communities and ecosystems is perceived as of utmost importance (Levine 2000; Chornesky and Randall 2003; Sax and Gaines 2003; Richardson and Pyšek 2006; Hejda et al. 2009; Winter et al. 2009). A small fraction of alien invaders change ecological functioning of invaded ecosystems resulting in further changes in the composition and structure of invaded communities (Richardson et al. 2000; Vilà et al. 2010). Invasive plant species have recently been shown to markedly differ in their effects on species richness and diversity of native species in invaded communities; some invaders reduce the numbers of native species that persist after the invasion only to a little extent (Hejda and Pyšek 2006, 2008) while others have considerable impact on native species richness (Hejda et al. 2009). Among the latter group, taxa of the genus *Fallopia* (syn. *Reynoutria*, Polygonaceae) can serve as an example of invasive plants imposing a great impact on native plant species diversity. The stands invaded by *Fallopia* taxa are species-poor, often monospecific (Sukopp and Starfinger 1995; Marigo and Pautou 1998). *Fallopia* taxa exhibit the most severe impacts on species richness and diversity among Central-European alien plants, reducing the number of species present prior to invasion by 66 to 86% (Hejda et al. 2009).

The genus *Fallopia* is native to Asia and several of the taxa are invasive in Europe (Beerling et al. 1994; Bailey and Conolly 2000; Bailey et al. 2007; Lambdon et al. 2008; Pyšek 2009) and other parts of the world (Seiger 1997; Randall 2002; Richards et al. 2008). *Fallopia sachalinensis* (F. Schmidt) Ronse Decr., *F. japonica* (Houtt.) Ronse Decr. var. *japonica* and their hybrid *F. ×bohemica* (Chrtek & Chrtková) Bailey, are rhizomatous herbaceous perennials producing a large amount of biomass (Brock 1995; Horn and Prach 1995) and large leaf area (Brabec and Pyšek 2000). They invade along water courses, in waste sites and other disturbed areas (Pyšek et al. 2001, 2002; Pyšek 2009). The invasion of *Fallopia* taxa is among the most intensively studied plant



invasions globally (Pyšek et al. 2008) and has been best documented from the United Kingdom, where it is supposed to have started in Europe (e.g. Bailey et al. 1995; Hollingsworth et al. 1998; Hollingsworth and Bailey 2000; Bailey and Conolly 2000), and from the Czech Republic (Pyšek and Prach 1993; Mandák et al. 2003, 2004).

The ecological understanding of *Fallopia* invasion and impact is still rather poor; it is usually attributed to a high growth rate (Marigo and Pautou 1998), prolific biomass production (Brock 1995; Horn and Prach 1995), good regeneration ability (Brock et al. 1995; de Waal 2001; Bímová et al. 2003; Pyšek et al. 2003) and its ability to grow at low nutrient levels (Adachi et al. 1996). Possible allelopathic effects of *Fallopia* taxa on germination of other species have not yet been assessed. The large amount of litter produced and the high rhizome density in the soil (Sukopp and Schick 1993) however indicates that this issue may be relevant, considering the low number of species occurring in invaded stands. Allelopathic effects of plant leaf litter were reported as a possible cause of inhibited germination and growth of tree seedlings (Rice 1984) and herbaceous woodland plants (Kuiters and Denneman 1987). Toxic action is attributed to phenolic compounds released from the litter (Rice 1984; Kuiters and Sarink 1986), and *Fallopia* species were reported to contain a large amount of these compounds, e.g. stilbenes, catechins and quinones (Inoue et al. 1992; Vrchotová et al. 2007). Phenolic compounds are known to inhibit not only germination, but also establishment and growth of other species in the community and can also be released into the soil from fresh living tissues such as rhizomes, root bark and leaves (Heisey 1990). In relation to plant invasions, allelopathy has been suggested as one of the underlying mechanisms on which the “novel weapon” hypothesis is based (Callaway and Aschehoug 2000; Hierro and Callaway 2003; Callaway and Ridenour 2004). Many studies have demonstrated the allelopathic effects of invasive plants on native species in their invaded ranges and provided compelling evidence for allelopathy as an important component of the competitive success of some of the world’s worst invaders (see Inderjit et al. 2008 and references therein).

The extremely low diversity of *Fallopia*-dominated communities may also be associated with the high cover of *Fallopia* canopy as it has been repeatedly reported that shading by a dense canopy inhibits germination of some plant species (e.g. Górski 1975; Górski et al. 1977; Bewley and Black 1982; Williams 1983; Pons 1992).

To obtain the first insight into the possible role of phytotoxic compounds and shading in reducing diversity of native species present in *Fallopia*-invaded stands, we assessed the effects of these factors on germination of co-occurring native species under laboratory conditions. By using extracts from above-ground and below-ground biomass of two *Fallopia* species and their hybrid, we determined (i) whether the chemical compounds inhibit the germination of two target species, a competitively strong native herb (*Urtica dioica*) and a grass (*Calamagrostis epigejos*), which are often dominant species prior to *Fallopia* invasion. Further, we aimed at assessing (ii) differences in potential phytotoxic action of particular *Fallopia* taxa that are known to differ in their invasiveness, (iii) differences in potential phytotoxic action of leaves and rhizomes, and (iv) explore how these effects are affected by simulated shading.

## Material and methods

### Target species

*Urtica dioica* L. is a perennial forb widely distributed in temperate regions (Hultén and Fries 1986). In the Czech Republic, its natural occurrence is in riparian sites where it grows as a dominant species in the summer in floodplain forest understorey. It also occurs as a dominant species of nutrient-rich ruderal habitats (Kopecký and Hejný 1992). In the field, it germinates from March to September. Its fruit (achene) stays dormant for 3–5 months after the collection and dry storage, which enhances germination (Nikolaeva et al. 1985). According to our preliminary tests, 70% of the seeds germinated in 25/10 °C after four months of cold stratification at 6 °C, with more germinating under white light conditions.

*Calamagrostis epigejos* L. (Roth), a rhizomatous perennial grass of Eurasian distribution (Rothmaler et al. 2002), is one of the most expansive species of the Czech flora, spreading remarkably in the last decades (Prach and Wade 1992). It is typical of disturbed human-made habitats and ruderal grasslands (Kopecký and Hejný 1992) and can grow on extremely acid substrata contaminated by toxic substances (Pyšek and Pyšek 1988). Preliminary tests in 25/10 °C revealed 90% germination after 5 months of dry storage, regardless of light regime. Fruits (caryopses) are produced in large quantities and germinate in the field in spring.

Besides the two native European taxa, an annual forb *Lepidium sativum* L., native to SW Asia and NE Africa (Hultén and Fries 1986) and commonly grown as a vegetable, was used. *Lepidium sativum* is very sensitive to allelopathic compounds, thus often used as a standard target species (Barnes and Putnam 1987; Heisey 1990; Kato-Noguchi and Ino 2001).

### Seed and tissue collection

Fruits of target species were collected in Prague, near the Modřanský brook valley (*U. dioica*) and along the road from Modřany to Cholupice village (*C. epigejos*) in September 1999. Seeds of *L. sativum* were obtained from a seed supplier. Fruits of *C. epigejos* and seeds of *L. sativum* were stored in paper bags in the dark at room temperature. Fruits of *U. dioica* were cold-stratified at 6 °C for four months before the start of the experiment.

Fresh rhizomes of the three *Fallopia* taxa were collected in February 1999 in Průhonice near Prague (49°59'41"N, 14°33'56"E). Fresh leaves, without any evident exterior sign of fungal infection, were collected at the same locality in July 1998 and dried at a room temperature.

## Extract preparation

**Aqueous extracts from dry leaves.** Maximum annual dry biomass produced by *Fallopia* in the study area is 228 g/m<sup>2</sup> (P. Pyšek et al., unpublished data). This value was used to set the upper limit of concentrations of phytotoxic compounds used in the experiment. Leaf biomass produced in the field was expressed per area of 75 mm Petri dish used for germination and volume of water it contained (8 ml). This calculation yielded 126 g of dry leaves per litre, i.e. c. 12.5% solution. However, since chemicals are released from leaf tissues gradually, we applied lower concentrations and used 25 and 50 g of dry leaves per litre, respectively, to produce 2.5% and 5% solutions, which is well within the concentration range of allelopathic studies (e.g. Kuiters and Denneman 1987). Dry leaves of *F. sachalinensis*, *F. japonica* and *F. ×bohemica* were ground, weighed and soaked in distilled water. The solutions were left for one week at 20 °C with occasional aeration to prevent anaerobic conditions (Kuiters and Denneman 1987), and then filtered through filter paper. Microbial degradation of the solution was not observed.

**Aqueous extracts from rhizomes.** Extracts were prepared from fresh washed rhizome cuttings and soaked in 100 ml of distilled water for one week at 20 °C, with occasional aeration to prevent anaerobic conditions. The solutions were filtered through filter paper. Amount of rhizome tissues used corresponded to 10, 20 and 30 g per litre, respectively, yielding 1%, 2% and 3% solution. Microbial degradation of the solution was not observed.

## Light regimes applied

Three light regimes were used. Light bulbs and fluorescent tubes provided a white light of 5000 L (105 mmol/cm<sup>2</sup>/s<sup>-1</sup>), simulating daylight in stands not covered by *Fallopia* species. Light filtered through canopy (green light) was simulated by using a single layer of green plastic reducing the red : far-red ratio by 69% and the photon flux density by 56% of white light levels (Skálová and Krahulec 1992); this regime simulated conditions under the *Fallopia* canopy. The standard procedure in germination experiments for creating dark conditions was used, by wrapping Petri dishes with germinating seeds in two layers of aluminium foil.

## Seed germination

Germination was tested in growth chambers. Seeds of *L. sativum* (25 seeds), *U. dioica* (50) and *C. epigejos* (50) were placed on two layers of filter paper in 75 mm diameter Petri-dishes and filled with 8 ml of leaf/rhizome extract or distilled water. Filter paper was used as a sterile medium. In the white- and green-light treatments, the evaporated water was replenished where it dropped below a standard mark. Dark treatments

wrapped in aluminium foil could not be filled-up with water during the course of the experiment, but the foil prevented any loss by evaporation. At the end of the experiment we ensured that the petri-dishes did not dry out.

All germination experiments were performed at fluctuating temperature of 25/10 °C (14 h light period/10 h-dark period). Germinating seeds were counted three times a week. Dark treatments were assessed at the end of the experiment, which was terminated after 21 days.

## Experimental design

The extracts were first used to conduct preliminary tests on the *L. sativum* seed bioassay. Germination was assessed under controlled conditions (distilled water), two concentrations of dry leaf extract (2.5 and 5%) and three concentrations of fresh rhizome extract (1%, 2% and 3%) of *F. sachalinensis*, *F. japonica* and *F. ×bohemica* with white light. Five replicates were used in each treatment. Since none of the three concentrations of rhizome extracts of the three *Fallopia* taxa had significant effect on germination of *L. sativum*, and seeds of the other two target species germinated up to 100% in most taxon/rhizome extract combinations, fresh rhizome extracts were not used in the main experiment as *L. sativum* is considered to be very sensitive to the allelopathic action.

In the main experiment, we used two concentrations (2.5% and 5%) of leaf extracts from *F. sachalinensis*, *F. japonica* and *F. ×bohemica*, and a control (distilled water = 0%). These combinations were assessed under three light regimes, to test germination response of the three target species, giving the total of 315 Petri dishes (6 taxon/concentration combinations + 1 control × 3 receiver species × 3 light regimes × 5 replicates).

## Statistical analysis

Data on the proportion of germinated seeds were angular transformed, and evaluated by fixed effect factorial ANOVAs. The preliminary test was done with a one-way ANOVA, using control and different concentrations of aqueous extracts from leaves and rhizomes of *F. sachalinensis*, *F. japonica* and *F. ×bohemica* as levels of a factor. Differences between control and each extract were assessed by t-tests. The main experiment was evaluated by three-way ANOVA, using the target species (*L. sativum*, *U. dioica* and *C. epigejos*), the light intensity (white, green, dark) and the concentration of aqueous extracts (control, 2.5 and 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica* and *F. ×bohemica*) as factors. A priori notions on differences among the concentrations within each target species and light intensity were tested by orthogonal contrasts (e.g. Sokal and Rohlf 1994). Calculations were done in the statistical software GLIM® (Crawley 1993| Francis et al. 1994).

## Results

The germination of target species varied under the combination of different treatments, from 8.0 to 100.0% in *L. sativum*, from 1.2 to 75.2% in *U. dioica* and from 6.4 to 97.3% in *C. epigejos* (Table 1). Germination was highly significantly affected by the interaction between target species, light regime and leaf extract concentration from the three *Fallopia* taxa (Table 2), and by the interactions between light and leaf extracts within each of the three target species (Table 3 and Fig. 1). In *L. sativum*, the 5% leaf extract from *F. japonica* markedly decreased germination in dark, but not in green and white light; the germination then increased on 2.5% extract from *F. japonica* in dark, but decreased in both light regimes. In *U. dioica*, the decrease in germination between control and 2.5% extract from *F. sachalinensis* was much steeper in light regimes than in dark. In *C. epigejos*, the germination in white light on 2.5% extract from *F. japonica* increased compared to control with no extract; on 5% extract from *F. japonica* germination increased in dark but decrease in both light regimes (Figure 1).

For each target species and light regime, one-way ANOVAs indicated that the germination differed highly significantly among the individual levels of extract concentration from the three *Fallopia* taxa (Table 4). Germination of control seeds also differed highly significantly from that of seeds exposed to extracts, with seed from control samples germinating to higher percentages than those exposed to extracts, except in *U. dioica* in the dark. Thus, *U. dioica* in the dark was the only target species unaffected by phytotoxic effect of extracts.

Within taxa, in all significant cases, 2.5% extracts had lower inhibitory effect than 5% extracts. Extracts from *F. ×bohemica* always produced highly significant differences in germination, and the same was true for extracts from *F. sachalinensis*, except for the effect on *U. dioica* in the white light. *Fallopia japonica* exhibited the weakest difference between concentrations of the extracts: the difference was signifi-

**Table 1.** Percentage germination of target species under different combination of light treatments (**WL** – white light; **GL** – green light; **Dark**), taxon (**FS** – *Fallopia sachalinensis*; **FJ** – *Fallopia japonica*; **FB** – *Fallopia ×bohemica*) and concentration of the solution (%).

Target species	<i>Urtica dioica</i>			<i>Calamagrostis epigejos</i>			<i>Lepidium sativum</i>		
	WL	GL	Dark	WL	GL	Dark	WL	GL	Dark
Control	69.6	70.8	20.8	89.6	90.4	97.3	100.0	100.0	100.0
2.5% FS	19.2	28.0	14.8	96.0	71.2	42.4	92.0	86.4	58.4
5% FS	6.8	8.0	1.2	29.6	20.0	12.0	23.2	35.2	8.0
2.5% FJ	73.2	75.2	68.4	96.0	64.0	38.0	96	98.4	100
5% FJ	67.6	51.2	28.8	72.8	20.0	53.6	96.8	96.0	48.8
2.5% FB	71.6	52.4	45.2	86.4	50.4	37.6	93.6	88.0	78.4
5% FB	15.2	28.0	4.8	21.6	6.4	11.2	36.0	59.2	12.0

**Table 2.** Three-way factorial ANOVA of angular-transformed proportions of germinated seeds for the target species (*Lepidium sativum*, *Urtica dioica* and *Calamagrostis epigejos*), light intensity (white, green, dark) and concentration of aqueous extracts (control, 2.5% and 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica* and *F. xbohemica*). The main effects (target species, light and concentration) and first-order interactions (target species) × (concentration), (target species) × (light), and (light) × (concentration), were not tested because the second-order interaction (target species) × (concentration) × (light) was statistically significant.

Source of variation	SS	df	MS	F
Target species	19.25	2	9.625	
Light	3.18	2	1.59	
Concentration	23.17	6	3.862	
(Target species) × (Concentration)	4.57	12	0.381	
(Target species) × (Light)	0.52	4	0.130	
(Light) × (Concentration)	0.80	12	0.0669	
(Target species) × (Concentration) × (Light)	2.01	24	0.08387	4.94 ***
Error	4.28	252	0.01698	
Total	57.78	314		

\*\*\* P < 0.001

**Table 3.** Two-way factorial ANOVAs of angular-transformed proportions of germinated seeds for the target species *Lepidium sativum*, *Urtica dioica* and *Calamagrostis epigejos*. The main effects of concentration (control, 2.5% and 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica* and *F. xbohemica*) and light (white, green, dark) were not tested because the first-order interaction of the main effects (concentration) × (light) were statistically significant.

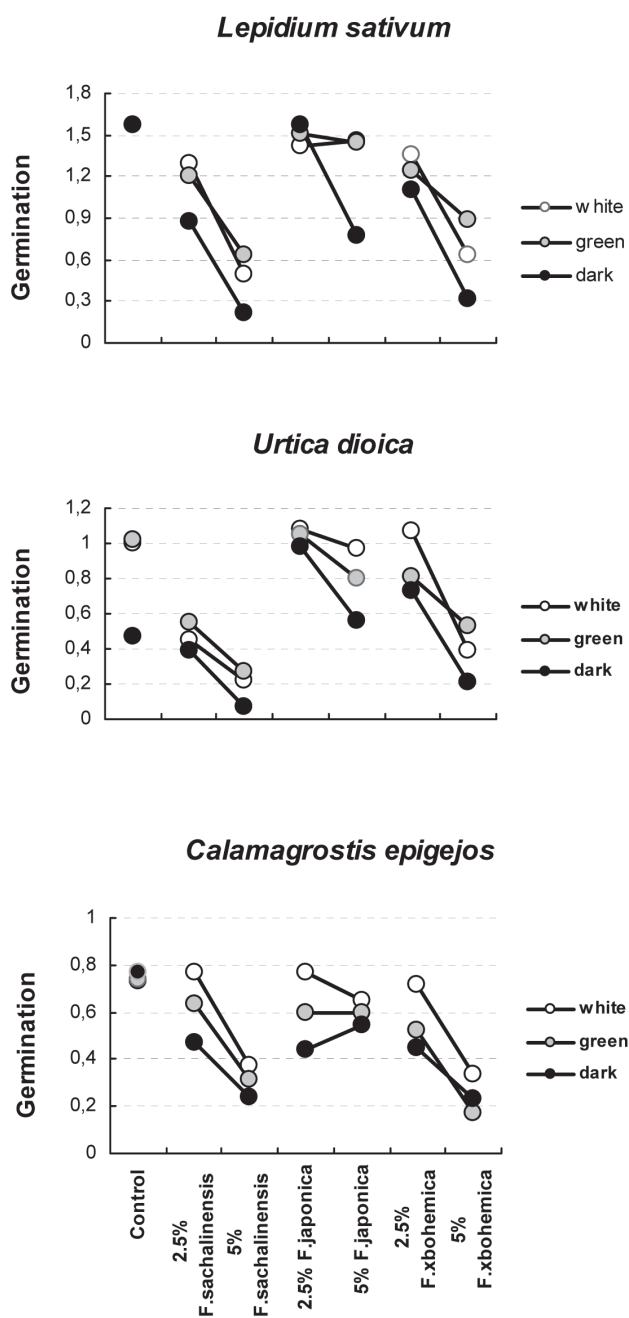
Source of variation	<i>Lepidium sativum</i>			<i>Urtica dioica</i>			<i>Calamagrostis epigejos</i>		
	df	MS	F	df	MS	F	df	MS	F
Concentration	6	2.703		6	1.426		6	0.493	
Light	2	0.907		2	0.682		2	0.260	
(Concentration) × (Light)	12	0.142	7.13***	12	0.068	2.74**	12	0.024	3.96***
Error	84	0.0199		84	0.0249		84	0.00613	

\*\*\* P < 0.001

\*\* P < 0.01

cant only in *L. sativum* in dark, in *U. dioica* in green light and in dark, and in *C. epigejos* in white light (Table 4).

Extracts from the three taxa, *F. sachalinensis*, *F. japonica* and *F. xbohemica*, always significantly differed in their effects on germination (Table 4). Ranked from the strongest to the weakest effect, the extracts from particular *Fallopia* taxa reduced germination in the order *F. sachalinensis* > *F. xbohemica* > *F. japonica* in *L. sativum* and *U. dioica*, and *F. xbohemica* > *F. sachalinensis* > *F. japonica* in *C. epigejos*.



**Figure 1.** Interactions of angular-transformed proportions of germinated seeds in the target species *Lepidium sativum*, *Urtica dioica* and *Calamagrostis epigejos*. The interactions between the concentration of aqueous extracts (control, 2.5 and 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica* and *F. xbohemica*) and light intensity (white, green, dark) are apparent as non-parallel lines of light intensity at each panel. See Table 2 for statistical significance of these interactions.

**Table 4.** One-way ANOVAs of mean angular-transformed proportions of germinated seeds at different concentrations of aqueous extract (control, 2.5% and 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica* and *F. ×bohemica*) and their orthogonal contrasts (control vs. extracts, *F. sachalinensis* vs. *F. japonica* vs. *F. ×bohemica*, and 2.5% vs. 5% dry leaf extract from *Fallopia sachalinensis*, *F. japonica*, and *F. ×bohemica*, respectively) for the target species (*Lepidium sativum*, *Urtica dioica* and *Calamagrostis epigejos*) at different light intensity (white light, green light, dark). Degrees of freedom for ANOVAs among concentrations are df = 6, 28; for the contrast control vs. extracts df = 1, 28; for the contrast *F. japonica* vs. *F. ×bohemica* df = 2, 28; and for the 2.5% vs. 5% dry leaf extracts df = 1, 28.

Source of variation	<i>Lepidium sativum</i>						<i>Urtica dioica</i>						<i>Calamagrostis epigejos</i>					
	White light		Green light		Dark		White light		Green light		Dark		White light		Green light		Dark	
	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS
Among concentrations	5.489	0.915***	3.576	0.596***	8.863	1.477***	4.139	0.690***	2.375	0.396***	2.860	0.477***	1.044	0.174***	1.182	0.197***	1.025	0.171***
Control vs. extracts	0.919	0.919***	0.746	0.746***	2.495	2.495***	0.401	0.401**	0.527	0.527***	0.0028	0.00280 ns	0.0758	0.0758**	0.297	0.297***	0.601	0.601***
<i>F. sachalinensis</i> vs. <i>F. japonica</i> vs. <i>F. ×bohemica</i>	1.690	0.845***	1.681	0.840***	2.124	1.062***	2.427	1.213***	1.305	0.652***	1.473	0.736***	0.179	0.0896***	0.315	0.157***	0.145	0.0723*
2.5% vs. 5% <i>F. sachalinensis</i>	1.608	1.608***	0.826	0.826***	1.087	1.087***	0.135	0.135 ns	0.194	0.194**	0.262	0.262***	0.385	0.385***	0.267	0.267***	0.135	0.135**
2.5% vs. 5% <i>F. japonica</i>	0.00483	0.00483 ns	0.0125	0.0125 ns	1.593	1.593***	0.0293	0.0293 ns	0.16	0.16**	0.438	0.438***	0.0350	0.0350*	0.00000	0.000000 ns	0.0240	0.0240 ns
2.5% vs. 5% <i>F. ×bohemica</i>	1.267	1.267***	0.311	0.311***	1.564	1.564***	1.146	1.146***	0.188	0.188**	0.685	0.685***	0.369	0.369***	0.303	0.303***	0.120	0.120**
Error		0.0175		0.0205		0.0218		0.0426		0.0183		0.0137		0.00577		0.00551		0.00731

\*\*\* P < 0.001, \*\* P < 0.01, \* P < 0.05, ns = not significant



## Discussion

### Potential for allelopathic effects in *Fallopia* taxa

Although the remarkably low species diversity in stands invaded by *Fallopia* is probably due to the competitive advantage resulting from its tall stature, rapid growth, dense rhizome system, and successful regeneration from rhizomes (Brock et al. 1995; Horn and Prach 1995; Bímová et al. 2003; Pyšek et al. 2003), constraints to germination of other species from phytotoxicity and shading may be another contributing mechanisms. The two target species tested, *Urtica dioica* and *Calamagrostis epigejos*, are among the most expansive native species in the Czech Republic (Prach and Wade 1992), dominating in riparian and ruderal habitats where *Fallopia* taxa often invade (Pyšek and Prach 1993; Brabec and Pyšek 2000). Both *C. epigejos* and *U. dioica* are competitively strong rhizomatous perennials forming large stands, but they also produce large quantities of seed (Prach and Wade 1992). In both species, this strategy of regeneration by seed is an effective means of long distance dispersal and colonization of new sites. Attempts to recolonize sites occupied by invasive *Fallopia* taxa might therefore be a common event in the disturbed landscapes where all taxa under question are abundant.

While the effect of light regimes on germination yielded inconclusive results, the interaction of light regime with the inhibitory effect of leaf extracts indicates that poor germination and establishment of native species in stands invaded by *Fallopia* taxa is unlikely to be explained by the effect of shading alone. However, our results demonstrate a pronounced phytotoxic effect of *Fallopia* taxa on germination of native dominant species under laboratory conditions. This inhibition presumably occurred through leaf chemical compounds, was affected by light regime, and its outcome under particular combination of factors depended on the species tested. As pointed out by Baskin and Baskin (1998), light filtered through the canopy can make seeds more sensitive to other environmental factors such as moisture, and thus organic compounds released into the soil could play a role in inhibiting germination until other environmental factors induce dormancy. Phenolic compounds released from leaf litter on the forest floor are permanently present in soil solution but their concentration varies in the course of the vegetation period (Lohdi 1975). Phenology thus plays a role in determining how the possible effect of allelochemicals and shading might operate on a given species. The effect of phenolic compounds is higher in early spring (Lohdi 1975) and for *Fallopia* species, early seasonal development is typical (Marigo and Pautou 1998). In temperate conditions of Central Europe, *Fallopia* quickly builds a dense leaf canopy from April to May (Brabec and Pyšek 2000).

Particular *Fallopia* taxa differed in their effect on germination of the target species. The weakest phytotoxic suppressor was *F. japonica*; its effect on both native dominants was generally lower than that of its two congeners, and higher phytotoxic concentration often did not result in a more pronounced effect. The weak phytotoxic effect of *F. japonica* corresponds to generally lower regeneration (Bímová et al. 2003) and

competitive ability of this species, compared to the other two *Fallopia* taxa (Brabec and Pyšek 2000). The most profound inhibitory effect was found for *F. sachalinensis*, which reduced namely the germination of *U. dioica*. The response of *U. dioica* to *F. ×bohemica* phytotoxins was between that of the two parent *Fallopia* species. Leaf extract of *F. sachalinensis* was previously reported to have other effects, such as stimulation of the synthesis of phenolic compounds in cucumber leaves (Konstantinidou-Doltsinis and Schmitt 1998; Daayf et al. 2000). *Fallopia ×bohemica* also profoundly inhibited germination, particularly that of *C. epigejos*. It may be thus hypothesized that the inhibitory effect of *Fallopia* taxa on germinating native species could be a factor favouring successful invasion.

### Limitations of the study

This study was based on using dry leaves, in order to simulate the situation in the field; leaves fall off *Fallopia* plants in dry conditions in the autumn and decomposition proceeds in winter. Although the use of freshly collected and subsequently ground dry leaf material in allelopathical studies has been criticised (Inderjit and Callaway 2003) because green leaves do not have the same properties as true litter and grinding might release compounds that naturally would not leach from leaf cells, this approach is being used to demonstrate the presence of the mechanism (Al Hamdi et al. 2001; Chon et al. 2003; Moradshahi et al. 2003). The present paper aimed at showing whether *Fallopia* above-ground plant parts could potentially inhibit germination of other plant species, and whether this potential differs among the congeners. Given its aim, the study was limited to laboratory conditions, but in order to demonstrate the real significance of the results in invaded communities, further research is needed in the context of soil ecology (Inderjit and Weiner 2001; Hierro and Callaway 2003; Inderjit and Callaway 2003; Inderjit and Nielsen 2003; Inderjit et al. 2008). When interpreting the results, it must therefore be borne in mind that concentrations of phytotoxic allelopathic compounds in the field might be lower than those applied in our study, due to the gradual leaching of compounds from leaves over time and spatio-temporal dynamics of this process (Lohdi 1975).

Our results, nevertheless, demonstrate that there is a strong potential phytotoxic effect of invasive *Fallopia* species on dominant native species and that this effect differs among the three taxa of this genus. Therefore, allelopathy cannot be excluded as one of the mechanisms contributing to the impact on the diversity of native species in *Fallopia*-invaded stands. The results of this paper further indicate that the light regime can influence the outcome of phytotoxic actions and should therefore be taken into account in studies focussing on allelopathic effects of plant species.

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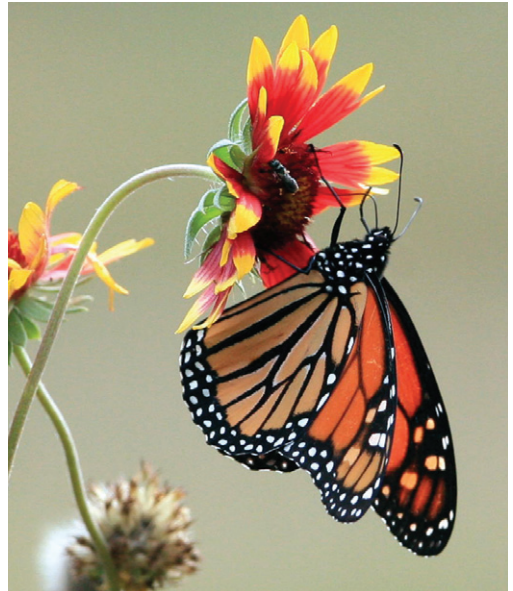
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# Secondary wind dispersal enhances long-distance dispersal of an invasive species in urban road corridors

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## Abstract

Roads contribute to habitat fragmentation and function as dispersal barriers for many organisms. At the same time many nonnative plant species are associated with road systems, a relationship that has been explained by the availability of disturbed habitats along roadsides and traffic-mediated dispersal of species. By studying secondary wind dispersal (SWD) over paved ground in an urban road corridor, we add the perspective of corridor-specific, but traffic-independent dispersal processes to the complex dispersal systems along roads. We analyzed (1) the seed shadow of an invasive tree *Ailanthus altissima* along a sidewalk subsequent to a strong wind and (2) the movements of painted samaras of this species released at ground level at the same site to identify the functioning of SWD. For the first experiment, we searched for samaras in the vicinity of an isolated tree three days after a strong wind. For the second experiment, we tracked the movement of the released samaras repeatedly over a period of 9–11 days, approximated probability-distance functions to the frequency distribution of samaras along the transect for different times after release, and related nearby measured wind data to changes in dispersal kernels. Single samaras from an isolated tree formed a seed shadow that extended for a distance of up to 456 m, and fragments of fruit clusters traveled up to 240 m. Forty-two percent of the sampled samaras were moved >100 m. The second experiment revealed that painted samaras released on the ground were moved up to 150 m over the pavement. Dispersal distances increased with time after seed release. A wider distribution of diaspores over the transect was significantly related to higher wind sums. Habitat shifts to safe sites for germination occurred during SWD, and different types of pavement influenced these processes. Smooth-surfaced pavement enhanced SWD, while cobbles with irregular surfaces slowed down or terminated SWD. During the observation period, 17% of released samaras accumulated in patches with a planted tree. Some were recaptured within the median strip and thus must have been lifted and moved over four lanes of heavy traffic. Our results suggest that impervious surfaces within road corridors can function as powerful avenues of wind-mediated long-distance dispersal and may counteract fragmentation of urban habitats. This also offers a functional explanation for the invasion success of *Ailanthus* at isolated urban sites.

**Keywords**

Alien species; anemochory; dispersal kernel; exotic species; habitat connectivity; seed tracking

**Introduction**

Roads contribute significantly to habitat fragmentation at local to regional scales and function as dispersal barriers for many species of plants and animals with consequences even at the evolutionary scale (Trombulak and Frisell 2000; Forman et al. 2002; Cheptou et al. 2008; Holderegger and di Giulio 2010). The level of fragmentation is especially high in urban settings (Robinson et al. 2005; Schleicher et al. 2011), but the ability to move in the urban matrix can counteract isolation effects as shown for many mobile animal species (Goddard et al. 2010). In plant species, human-mediated dispersal has been recognized as a powerful driver of long-distance dispersal leading to range expansion in many introduced species (Hodkinson and Thompson 1997; Kowarik and von der Lippe 2007). Despite this, human-mediated dispersal processes have barely been quantified in terms of dispersal distances (Carlton and Ruiz 2005), although a better understanding of mechanisms that drive long-distance dispersal (LDD) is crucial for assessing invasion processes and management options (Pyšek and Hulme 2005).

Since the pioneer work by Clifford (1959), several studies have illustrated the functioning of traffic-related dispersal by quantifying the number of species moved by vehicles. Propagules of plant species can travel either via mud-mediated adhesion to vehicles or in windshield wiper grooves and similar parts of vehicles (Schmidt 1989; Hodkinson and Thompson 1997; Zwaenepoel et al. 2006; von der Lippe and Kowarik 2007a). In addition, spillage from transports of harvest or seeds functions as an effective dispersal vector for crop species (von der Lippe and Kowarik 2007b; Kawata et al. 2009).

The efficiency of traffic-related dispersal in terms of seed rain and spatial reach has been recently quantified by sampling urban highway tunnels in Berlin. Vehicles moved 204 species, i.e., 12.5% of the total flora of Berlin. The share of transported native and nonnative species was the same, but long-distance dispersal was significantly more frequent in nonnative than in native species (von der Lippe and Kowarik 2007a). Vehicles moved propagules of more species, and more seeds of nonnative species, along outbound lanes than along inbound lanes (von der Lippe and Kowarik 2008). These results clearly illustrate a powerful role of traffic as dispersal pathway for introduced species. In addition to vehicles, people can also move species over long distances along road corridors directly via attachment of propagules to footwear or clothing (Mount and Pickering 2009; Wichmann et al. 2009).

Distribution patterns at regional scales illustrate that many nonnative plant species are associated with the road system (Gelbard and Belnap 2003; Dark 2004; Pauchard and Shea 2006). Correspondingly, range extension of invasive species has often been observed along roads (Ernst 1998; Lavoie et al. 2007; Jadoin et al. 2008; Essl et al. 2009; Pauchard et al. 2009), and increasing traffic or human mobility relates to the

vector strength (Parendes and Jones 2000; Gelbard and Belnap 2003; Niggemann et al. 2009). Roadsides are also known to function as foci for the invasion of adjacent habitats (Tyser and Worley 1992; Gelbard and Belnap 2003). A better understanding of underlying mechanisms is thus an important challenge in invasion research.

Yet unfolding the mechanisms that drive plant invasions within road corridors requires disentangling the role of site- and vector-dependent mechanisms, as both may enhance plant migration along transportation systems. Plant dispersal and establishment along transport routes are mutually dependent processes. Habitats within road corridors are usually subject to high disturbance and provide safe sites for the establishment of numerous nonnative species (Hansen and Clevenger 2005; Rentch et al. 2005). Roadside habitats can thus favor the establishment of populations of species that are dispersed by vehicles and can, in turn, act as seed sources for subsequent adhesion to vehicles as shown by our previous study: the species composition of the sampled tunnel seeds was more similar to the regional roadside flora of Berlin than to the local flora around the tunnel entrances (von der Lippe and Kowarik 2007a).

In urban settings, roadside vegetation is mostly confined to habitats around planted street trees, joints and crevices in the pavement, and narrow strips with pervious surfaces either along the traffic lanes or adjacent to built structures (e.g., Langer 1994; Wittig and Becker 2010). Impervious surfaces of traffic lanes, sidewalks, or bicycle lanes clearly prevail in urban road corridors. Such sites are mostly perceived as hostile environments for plant dispersal and establishment and can even drive short-term evolutionary adaptation as shown for *Crepis sancta*, an herb that produces both dispersing and non-dispersing seeds. Patchy urban populations around trees showed a higher number of non-dispersing seeds compared to rural populations, which suggests a rapid evolution towards non-dispersing dispersal types in fragmented urban sites to prevent costs of dispersal losses over impervious urban surfaces (Cheptou et al. 2008).

Yet the escape of propagules in local populations that are embedded in a matrix of impervious urban surfaces could also lead to the establishment of new populations—assuming that propagules reach safe sites for germination within or adjacent to the road corridor. Here, the question arises whether or to what extent sealed urban surfaces hinder or enhance the secondary dispersal of propagules by wind after they have landed on the ground.

Secondary dispersal is generally acknowledged to be an important mechanism (Higgins et al. 2003), and studies on secondary wind dispersal over natural surfaces covered with snow (Matlack 1989) or in arid regions with sparse vegetation (Schurr et al. 2005) suggest a high potential for LDD in propagules after they have landed on the ground. We hypothesize that sidewalks and other linear structures with paved surfaces along roads may function—analogously to natural surfaces with missing or few barriers to seed transport—as avenues of secondary wind dispersal and may thus help to overcome spatial isolation of patchy urban habitats. We thus aim to add the perspective of corridor-specific, but traffic-independent dispersal processes to the complex dispersal systems functioning in road corridors.

To study secondary wind dispersal over impervious urban surfaces, we chose the tree *Ailanthus altissima* (henceforth *Ailanthus*) as model species. *Ailanthus* is native to China and northern Vietnam and invades urban and non-urban transport corridors in many regions worldwide with a temperate or Mediterranean climate (Kowarik and Säumel 2007). Colonized habitats include medians, cracks and crevices of sealed surfaces, patches with planted trees and, outside of cities, roadside habitats (Singh et al. 1992; Lenzin et al. 2001; Huebner 2003; Merriam 2003; Rentch et al. 2005). These patterns suggest the availability of safe sites for germination as well as an efficient dispersal in road corridors, but the functioning of different site- or dispersal-related mechanisms has not been disentangled thus far.

Samaras of *Ailanthus* are primarily dispersed by wind during a long and highly variable period of seed abscission that can extend until the next summer (Bory and Clair-Maczulajtys 1980). It remains an open question, however, whether wind plays a role as a secondary vector in moving samaras in addition to its function as a primary vector. Observation of wind-mediated seed transport in traffic corridors is anecdotal thus far.

To shed light on this mechanism, we first analyzed the seed shadow of an isolated tree in an urban road corridor and then performed a second experiment, releasing samaras at ground level, to quantify the role of secondary wind dispersal in road corridors. Diaspores are typically moved several times during secondary dispersal processes and may reach their final destination only after a considerable length of time. Following this process requires methods of direct seed tracking because seed traps would stop the dispersal process (Bullock et al. 2006). We therefore painted propagules of *Ailanthus* and released them in the same road corridor to track their movement over paved surfaces over a period of up to 11 days. We hypothesized that propagules of *Ailanthus* are repeatedly moved over paved urban ground and may overcome spatial isolation of patchy urban habitats by that dispersal pathway.

## Methods

### Seed shadow

Three days after a strong wind in March 2005 (maximum speed 7.7 m/s), we studied the seed shadow of an isolated *Ailanthus* tree along a section of the major urban road corridor “Unter den Eichen” in southwest Berlin, Germany, which runs in the direction of the prevailing winds (Fig. 1). Over a distance of 600 m, we sampled a strip 0.43–0.6 m wide that formed the border between the paved sidewalk area and the adjacent lots; the total sidewalk width between the traffic lanes and the adjacent private lots was 6–7 m. Over most parts of the sampled section, a wall with a fence on the top separated the paved public right-of-way from the private area, and corner blocks marked this boundary over the remaining parts. To increase the chance of identifying corridor-specific but traffic-independent dispersal processes we sampled that part of the sidewalk that was least exposed to traffic. The sampled strip was paved with small



**Figure 1.** **A** Urban road corridor “Unter den Eichen” in Berlin with an isolated tree of *Ailanthus altissima* as seed source. The red arrow indicates the sampled seed shadow in the prevailing wind direction; the lawn on the right side is part of the median **B** Habitats along the sidewalk. The site for the release experiment is marked by a circle with an X. Samaras were repeatedly tracked after release for their presence in different habitat types: H1, H3 – sidewalk pavement with small granite cobbles and large joints; H2 – sidewalk pavement with even surfaces and small joints; H4 – patches of open ground around planted trees, sparsely covered with ruderal vegetation; H5 – margin of the adjacent traffic lane close to the curb.

granite cobbles with a surface of about 5 x 7 cm, leaving joints about 0.5–1.5 cm wide in between (Fig. 1). The 8-m-tall *Ailanthus* tree grew in a garden close to this wall and parts of the crown stretched out in the road corridor. Hence, propagules were expected to reach the road corridor easily by primary wind dispersal.

We quantified the seed shadow of *Ailanthus* in segments of 20 meters and differentiated two types of propagules that are known to be dispersed by wind: single, one-seeded, spirally twisted samaras and fragments of panicles that can harbor up to 500 samaras prior to fragmentation during the abscission period (Bory and Clair-Maczulajtys 1980). Samaras from populations in Berlin average 4.7 cm in length and 0.9 cm in width (Kowarik and Säumel 2007). We did not measure the individual weights of the samaras because previous studies suggested that this parameter is not correlated with dispersal (Landenberger et al. 2007) or germination success (Delgado et al. 2009).

As we were only able to sample the seed shadow three days after the strong wind, the observed distribution of samaras along the sidewalk integrates the functioning of primary wind dispersal and subsequent wind-mediated lateral transport of samaras. To disentangle the contribution of the latter, i.e., the secondary dispersal pathway, we performed a release experiment at the same site.

### **Release experiment**

At the same location, we placed three cohorts of samaras on consecutive days on the paved sidewalk and observed their lateral transport by wind for 9–11 days (Fig. 2). The first cohort had 70 samaras, each of the other cohorts had 100. We sprayed the samaras of the different cohorts with different colors to track their movement in time and space. As paint adds weight, the observed transport distances are likely underestimated. An experiment on a concrete surface in a wind tunnel allowed this effect to be quantified. Painting increases the mean lift-off velocity of 3.3 m/s in samaras of *Ailanthus* by 6–7% (Lemke et al. 2009).

Each day after release, we determined the transport distances along the sidewalk in the main wind direction and in the opposite direction. We determined the presence of samaras in different types of habitats as shown in Fig. 1b to assess their role in promoting or terminating secondary wind dispersal in road corridors. We also searched the adjacent habitats (traffic lanes, front gardens, median strip of the main road) for samaras that might have left the area of the sidewalk.

### **Measurement of wind**

As we were not able to measure the wind speeds during the observation period at the release site, we used wind data collected on the roof of the nearby building of the Department of Ecology at a height of 23 m. The distance to the release site was only about 1 km, but wind conditions there may diverge from the measured data, mainly due to lateral and horizontal turbulence that frequently occurs in urban road corridors



**Figure 2.** **A** Fragmented fruit cluster as component of the seed shadow **B** Release site with the first cohort of painted samaras **C, D** Joints between granite cobbles and vegetation around planted trees as potential safe sites for germination.

(e.g., Zajic et al. 2011). The wall that bordered the sidewalk along most parts of the sampled section, for example, likely led to increased wind speeds. Yet as the measured data are supposed to represent differences in the local wind field we use them as proxies for relative differences in wind speed between different survey dates.

We therefore calculated wind sums, that is, the cumulative wind speed in the main wind direction over all measurement times, wind maxima, and wind sums for wind measurements that exceeded a speed of 3.7 m/s, which was measured in a wind tunnel as the minimum wind speed that could move painted samaras of *A. altissima* over the ground (Lemke et al. 2009).

### *Statistical analyses*

Probability-distance functions were approximated to the frequency distribution of samaras along the sidewalk for different times after release. We pooled data of the first and second days, the third to fifth days and the sixth to eleventh days of all three cohorts to reveal differences in the shape of dispersal kernels in relation to time after release. Functions were fitted by non-linear regression using the log-normal function (Eqn. 1), which usually approximates wind dispersal data very well (Jongejans et al.

2008). In this equation  $r$  is the distance from the release site and  $f(r)$  the probability that a diaspore will be dispersed at that distance. The shape parameter  $b$  provides information about the skewness of the dispersal kernels, with lower values of  $b$  representing more right-skewed distributions. Increasing values of the scale parameter  $a$  represent a wider distribution of diaspores over the transect.

Eqn. 1:

$$f(r) = \frac{1}{b (2\pi)^{1/2}} \exp\left(-\frac{[\log r - a]^2}{2b^2}\right)$$

To relate wind data to the change in dispersal kernels, we fitted a lognormal function to the seed distribution of each single survey date, separately for each cohort of samaras. We then calculated changes between the location of the peak of the curves, the shape parameter  $b$  and the scale parameter  $a$  of the lognormal models for each two subsequent survey dates. As all parameters are probably affected by wind dispersal over the ground, these changes were related to wind sums and wind maxima that occurred between the two survey dates by linear regression. All analyses were performed with the statistical and programming language R 2.10 (R Development Core Team 2009). The package *nls* was used for nonlinear regression.

## Results

### Seed shadow

The seed shadow from the isolated *Ailanthus* tree, sampled after a strong wind, extended for 456 m along the sidewalk. Only 2% of all propagules were sampled in the direct vicinity (0–20 m) of the parent tree. The majority (58%) were moved up to 100 m, about one-third (34%) up to 200 m, 6% up to 300 m, and the remaining 2% up to 456 m from the parent tree (Fig. 3, Table 1).

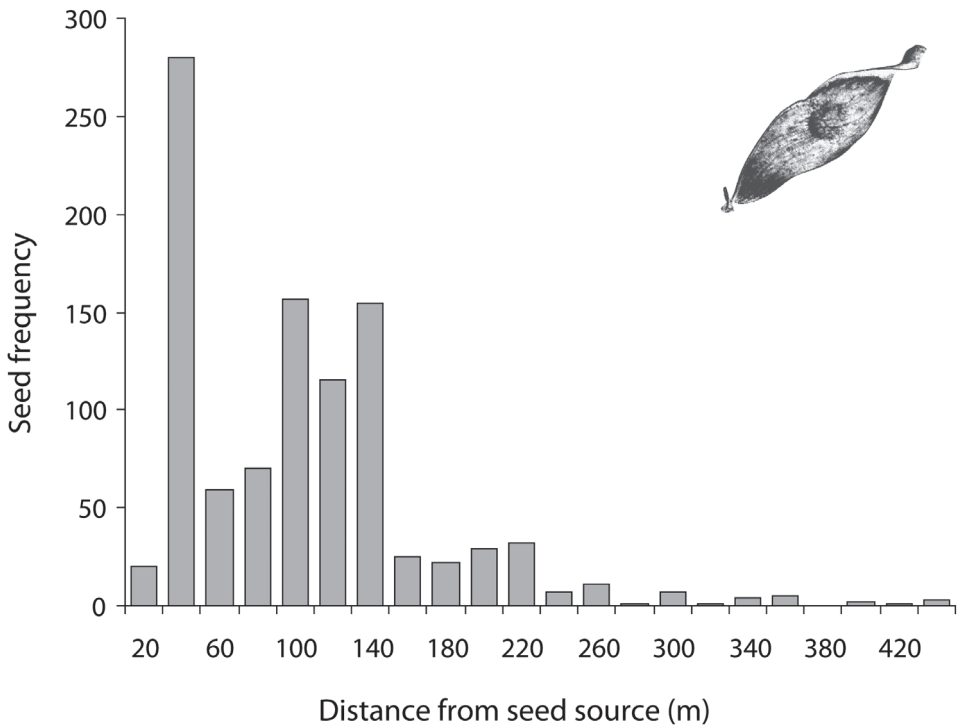
Single samaras dominated the total of sampled propagules (85.2%). The remaining 14.8% were moved as fragmented parts of fruit clusters, up to a maximum distance of 240 m from the parent tree. The 16 cluster fragments had on average 9.4 samaras. The three largest clusters with 31–53 samaras were sampled at distances of 30–130 m from the seed source (Tables 1, 2). Single samaras were transported over longer distances than fruit clusters (Table 1).

### Release experiment

#### *Recapture rates and extent of secondary wind dispersal*

The mean recapture rate of the released cohorts of samaras was 82.3% one day after release and decreased to 38.1% at the end of the experiment, 9–11 days later. Hence,





**Figure 3.** Seed shadow from an isolated *Ailanthus altissima* tree in an urban road corridor after a strong wind in March 2005. Propagules were recorded for 20-m sections of a sidewalk in the main wind direction. The peak in the 40-m section coincides with the presence of a bus shelter that clearly encouraged the accumulation of samaras.

62% of the exposed samaras vanished from the study area. Most of the samaras (72.4% of those recaptured one day after release) were found in the main wind direction along the sidewalk. Only a few samaras (9% one day after release) were transported in the opposite direction to an average distance of 30 m from the release site (one up to 50 m), and one percent were found on the median strip. Over the total observation period, wind moved the released samaras up to 150 m in the main wind direction along the sidewalk.

### *Shape of the dispersal kernel and transformation over time*

The distribution of samaras along the transect followed a right-skewed humped curve with a peak at approximately 10 m between the first and second days of exposure and at approximately 20 m between the 6th and 11th days (Fig. 4a). The distance of the peak of the fitted dispersal kernel from the starting section, where the diaspores were laid out, increased significantly with time of exposure (Fig. 4b). Its location along the transect in the main wind direction shifted from a minimum of 3.2 m after one day to a maximum of 28.2 m after 11 days. Also the shape parameter  $b$  and the scale pa-

**Table 1.** Single samaras and samaras in fragmented fruit clusters as components of a seed shadow from an isolated *Ailanthus altissima* tree sampled after a strong wind in March 2005 in an urban road corridor.

Distance from seed source (m)	All samaras		Single samaras		Samaras as part of fruit clusters		
	n	%	n	% of all samaras moved this distance	Samaras (n)	Fruit clusters (n)	% of all samaras moved this distance
0–100	586	58.2	494	84.3	92	12	15.7
100–200	346	34.4	289	83.5	57	3	16.5
200–300	58	5.8	56	96.5	2	1	3.5
300–400	12	1.2	12	100			
400–456	4	0.4	4	100			
Total	1006	100	855		151	16	

**Table 2.** Number, size, and maximum transport distance of fruit clusters of *Ailanthus altissima* as components of a seed shadow along an urban sidewalk after a strong wind in March 2005.

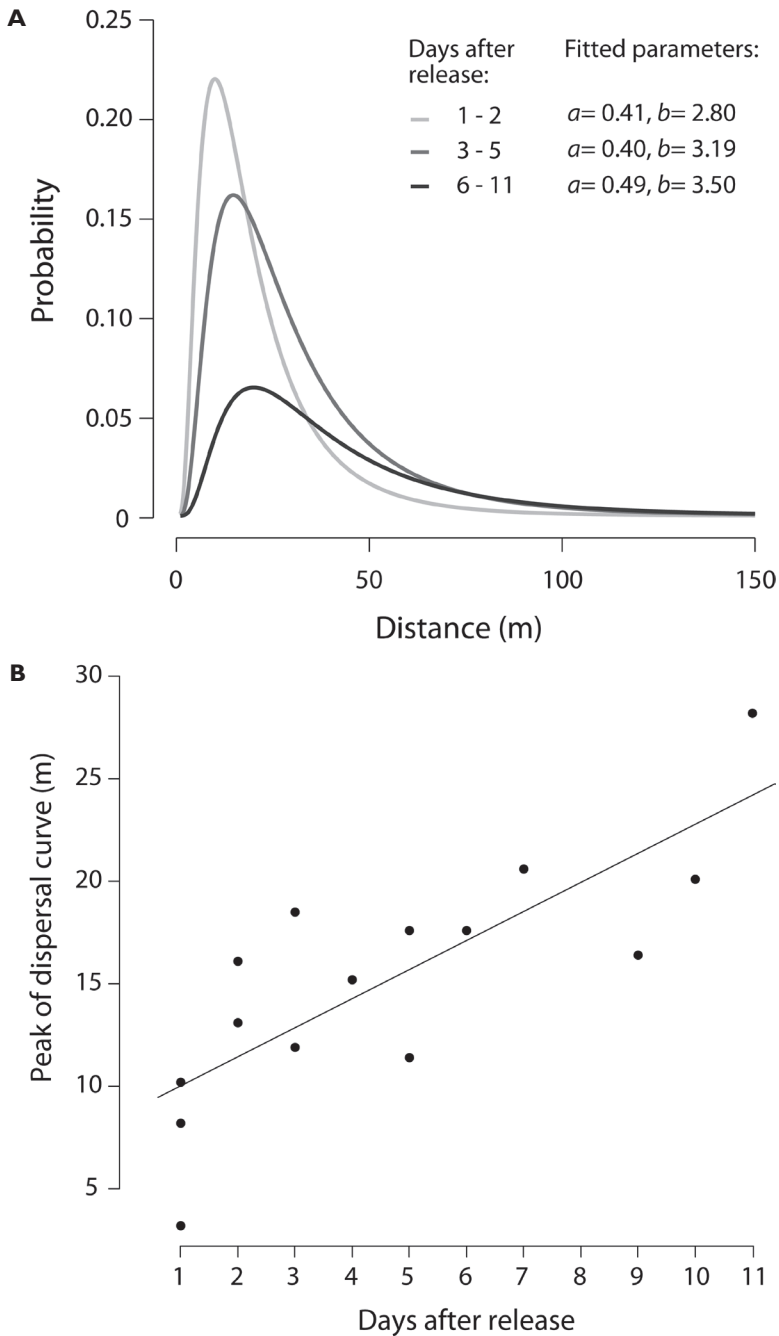
Samaras per fruit cluster (n)	2	3	8	31	34	52
Clusters (n)	10	2	1	1	1	1
Observed maximum transport distance (m)	240	140	30	30	30	130

parameter  $a$  of the fitted lognormal models significantly increased with time of exposure (linear regression,  $p = 0.005$  and  $p = 0.002$  respectively).

While no significant relation between wind parameters and change in the location of the peak and the shape parameter of the fitted dispersal kernels was revealed, the change in the scale parameter  $a$  was significantly positively related to the sum of the measured wind speeds that were above the threshold of 3.7 m/s (Table 3). Hence, wind sums above the threshold to move a samara over paved surfaces showed a significant influence on distributing samaras over a wider section of the transect.

### *Habitat shifts*

Within a period of 9–11 days, secondary wind dispersal resulted in conspicuous habitat shifts within the road corridor (Table 4). All exposed samaras vanished from the release site, and 7% of these remained in the paved strip with large joints between the granite cobbles, the habitat type in which the samaras were initially released (see Fig. 2). About 29% of all released samaras crossed the neighboring pavement with small joints, but no samara remained on this surface. Most of them (17%) were recaptured in adjacent patches with planted trees and another 3% in the pavement between these tree patches. This area had the same habitat structure as the pavement around the release site. About 10% of the released samaras were found at the edge of the traffic lane, close to the curb that serves as a border of the sidewalk area.



**Figure 4.A** Probability-distance distribution of samaras of *Ailanthus altissima* in the main wind direction after three different time spans of seed release in a paved road corridor (estimated by a lognormal function from three cohorts) **B** Effect of time after release on the location of the peak of the fitted dispersal kernel (lognormal function) along the road transect in the main wind direction. The least squares regression line is shown ( $y = 1.42x + 8.6$ , Adj.  $R^2 = 0.60$ ,  $p < 0.001$ ).

**Table 3.** Linear regression models for the relation between wind parameters and the change in the location of the peak, and in shape and scale parameters for the fitted lognormal dispersal curves of subsequent sampling dates. The shape parameter  $b$  indicates the skewness of the dispersal curve, the scale parameter  $a$  indicates the dispersion of diaspores along the entire transect. Wind speeds and maxima were recorded at a nearby weather station over the period between each two sampling dates. The wind speed of 3.7 m/s was recorded as the average wind speed that caused any movement of samaras of *Ailanthus altissima* on a paved surface in a wind tunnel experiment (Lemke et al. 2009). Significant regression models are in bold.

	Coefficient	P-value	Adj. R <sup>2</sup>
Dependency of $\Delta$ peak (change in location of the peak) on:			
Maximum wind speed	1.9727	0.338	<0.01
Wind sum	-0.0058	0.419	-0.03
Wind sum > 3.7 m/s	0.0153	0.089	0.19
Dependency of $\Delta b$ (change in shape parameter) on:			
Maximum wind speed	0.0017	0.874	-0.09
Wind sum	>0.0001	0.994	-0.01
Wind sum > 3.7 m/s	>0.0001	0.671	-0.08
Dependency of $\Delta a$ (change in scale parameter) on:			
Maximum wind speed	0.1787	0.112	0.16
Wind sum	-0.001	0.092	0.18
<b>Wind sum &gt; 3.7 m/s</b>	<b>0.0025</b>	<b>0.008</b>	<b>0.47</b>

**Table 4.** Habitat shifts in three cohorts of samaras of *Ailanthus altissima* due to secondary wind dispersal in an urban road corridor 9–11 days after release at ground level on the pavement (habitat type H1). For the spatial arrangement of habitat types H1-5, see Fig. 1b.

	% Cohort 1 (n = 70)	% Cohort 2 (n = 100)	% Cohort 3 (n = 100)	Mean
Days after release	11	10	9	
Release site	0	0	0	0
Pavement with large joints (H1)	2.9	5	14	7.3
Pavement with small joints (H2)	0	0	0	0
Pavement with large joints (H3)	2.9	0	6	3.0
Tree patches (H4)	24.3	11	15	16.8
Margin of traffic lane (H5)	11.4	8	9	9.5
Median strip (lawn) beyond four traffic lanes	2.9	1	0	1.3
Total recaptured	44.4	26	44	38.1
Total vanished	55.6	74	56	61.9

Surprisingly, a total of nine samaras (3.3%) emerged on the median strip during the observation period, eight on a mowed lawn and one at the edge of the traffic lane, close to the curb. Two of these samaras still remained on the lawn of the median strip at the end of the observation period while the others continued their travels to unknown destinations.

## Discussion

Long-distance dispersal is crucial for the spread of many invasive species but is usually difficult to observe due to the rarity of LDD events and the fact that propagules are often dispersed by more than one vector over longer periods of time (Higgins and Richardson 1999; Bullock and Clarke 2000; Ozinga et al. 2004). Our model species, *Ailanthus altissima*, is primarily dispersed by wind, but dispersal by water has recently been revealed as a further important dispersal process (Kaproth and McGraw 2008; Kowarik and Säumel 2008; Säumel and Kowarik 2010). Secondary wind dispersal in *Ailanthus* has been studied thus far only in natural settings, revealing negligible transport distances: within 27 days, no samara travelled > 0.25 m along the floor of a closed canopy forest with a 9% slope, and on a 48% slope only about 6% of all samaras were moved between 0.25 and 10 m (Kaproth and McGraw 2008). These results are not surprising because dense vegetation usually hampers secondary wind dispersal (Redbo-Torstensson and Telenius 1995). Our study demonstrates the importance of secondary wind dispersal in road corridors, i.e., in linear habitats with more or less smooth surfaces and usually sparse vegetation.

### *Primary versus secondary wind dispersal*

Previous experiments and modeling studies suggest that primary wind dispersal rarely covers transport distances of more than 100 m, while secondary wind-mediated dispersal processes may move seeds over larger distances—a result that is usually attributed to stochastic processes (Matlack 1989; Higgins et al. 2003; Soons et al. 2004; Schleicher et al. 2011). The analysis of the seed shadow of an 8-m-tall isolated tree revealed a maximum distance for seed travel of 456 m (Table 1), which likely results from the combined functioning of primary dispersal by a strong wind and secondary wind-mediated dispersal of fallen samaras over a period of three days.

The maximum transport distance observed in the first experiment clearly extends the values reported for primary wind dispersal alone measured by using seed traps. A field study covering 6 months found that wind moved samaras at least 200 m over a hay field, with four 18-m-tall trees as seed sources (Kota 2005; Landenberger et al. 2007). As in many wind-dispersed species, there was a strong decline in seed density with increasing distance from seed sources. Landenberger et al. (2007) found a log-linear decrease in mean seed density per square meter with increasing distance from the seed source. Correspondingly in a Korean urban study, 75% of seedlings were found within 20 m of the parent tree, with single seedlings to a distance of about 65 m (Cho and Lee 2002).

Yet in our study, about 42% of the sampled seed shadow had been moved over distances of >100 m, a distance which is often used to define long-distance dispersal (Table 1). As the observed seed shadow integrates both primary and secondary wind dispersal over a period of three days, we tracked the movement of painted samaras to isolate the functioning of secondary wind dispersal over paved ground. Over the observation period, between 1 and 5.7% of the three released cohorts of samaras were

moved at least 100 m over ground, with a maximum distance of 150 m from the release site. As painting reduces the lift-off velocity of samaras by 6–7% (Lemke et al. 2009), the true transport distances achieved by secondary wind dispersal are likely higher. Considering the modest wind speeds during the release experiment the measured transport distances are probably not rare events in road corridors but occur rather frequently in such habitats.

Hence, secondary wind dispersal alone can move *Ailanthus* samaras over long distances in urban road corridors, and a combined functioning of primary and secondary wind dispersal achieves transport distances far beyond those due to primary wind dispersal alone. Considering the negligible wind-mediated transport distances of samaras on a forest floor (less than 10 m; Kaproth and McGraw 2008), our study also adds evidence to the context specificity of secondary dispersal processes. Apparently, the specific habitat characteristics of urban road corridors, i.e. linear habitats with even surfaces and a high probability of increased wind turbulence, enhance secondary wind dispersal—a process which is often underestimated as it cannot be measured by traditional seed trap experiments. Yet this dispersal pathway is common in urban settings, and our study shows that it is well accessible to modelling approaches—as are other secondary dispersal processes (e.g., Schurr et al. 2005; Wichmann et al. 2009).

Figure 4 illustrates secondary wind dispersal of exposed samaras as a continuous process. With increasing time of exposure, the peak of the modeled dispersal curves shifts to higher distances. At the same time, a wider dispersion of diaspores along the sidewalk occurred, expressed by the increase in the scale parameter  $a$  of the fitted lognormal function. Also the shape of the dispersal curve changes with time from a strongly to moderately right-skewed distribution. This goes along with a loss of diaspores from the study area, which we couldn't control for in this experiment. The fate of these lost samaras remains unknown. It is likely however that at least a small proportion of these “losses” were transported beyond the borders of the study area to suitable germination sites.

The morphology of the samaras obviously facilitates wind-mediated lateral transport, likely because the twisted shape of the samaras increases the surface exposed to wind. Resulting movements can proceed with or without further rotations along the longitudinal axis. It is thus an open question whether our results can be generalized for other species with other seed morphologies.

In our release experiment, we found no significant relation between total wind sums and wind maxima and any change in parameters of the fitted dispersal kernels. This may be due to the mismatch between the wind data—measured nearby—and the local variation of the wind field in the studied road corridor. Yet the significant increase in the scale parameter  $a$  with higher wind sums above 3.7 m/s demonstrates the potential of wind to distribute diaspores over the pavement when the threshold for movement over the ground is exceeded. This is in accordance with the only existing mechanistic model for wind dispersal over the ground that accounts for a threshold in wind speed beyond which movement of diaspores is possible (Schurr et al. 2005).

As neither the change in the location of the peak nor the estimated shape parameter  $b$  showed significant dependencies on wind sums above 3.7 m/s, higher wind sums are not necessarily related to an increase in secondary dispersal distances in urban road corridors. This can be explained by the turbulent character of wind in road corridors. While wind speed is generally reduced in urban regions, turbulence often occurs in road corridors (Zajic et al. 2011), making the direction of wind dispersal over the ground more unpredictable than in open landscapes.

Vertical turbulence has been found to function as an important driver of LDD in propagules of herbaceous species with falling velocities < 0.5–1.0 m/s (Tackenberg et al. 2003). The value for *Ailanthus* is within this range (0.56 m/s; Matlack 1987). We did not directly observe vertical updraft of samaras, but our experiment provides indirect evidence of the functioning of this mechanism. A few samaras were moved from the sidewalk to the median strip of the road and must thus have been lifted over four lanes of heavy traffic and a curb that formed the border of the lawn on the median strip. During this travel, wind turbulence induced by vehicles may have enhanced the updraft of samaras, a phenomenon observed elsewhere (von der Lippe, pers. observ.).

### *Transport of single and clustered samaras*

Within the sampled seed shadow, single samaras were generally transported over longer distances than fragments of fruit clusters with two and more samaras, but interestingly, clumps with more than one samara traveled up to 240 m from the seed source (Table 2). This is the first evidence of LDD of clustered samaras. The dispersal of such clumps can result in patches of closely related seedlings (Pan and Bassuk 1985), which can be advantageous for the occupation of safe sites and for establishing pioneer populations owing to an increased probability of germination of one or more seeds. As *Ailanthus* is a strictly dioecious tree (other reports appear to be wrong; Kowarik and Säumel 2007), the arrival of more than one seed at an isolated site could lead to the establishment of individuals of different sexes and thus enhance sexual regeneration.

### *Habitat shifts and potential safe sites*

Studies on secondary wind dispersal in (near-)natural settings have shown that the density and structure of vegetation as well as morphological variation of the ground strongly affect the travel of propagules (e.g., Matlack 1987; Redbo-Torstensson and Telenius 1995; Schurr et al. 2005). Our study demonstrates that slight variations in the structure of paved surfaces also shape the dispersal processes in urban road corridors. During the observation period, conspicuous shifts occurred between habitats (Table 4). The crucial question for seedling establishment subsequent to dispersal is which of these can function as safe sites for germination.

The sidewalk was composed of two types of pavement that paralleled the traffic lanes (Fig. 1). About 10% of the exposed samaras remained in the strips with small granite cobbles, with most captured in the large joints between these cobbles. No sa-

mara remained on the adjacent pavement type with smooth-surfaced paving and very small joints in between. Yet the vast majority of the exposed samaras must have been moved over this surface because they were recaptured in habitats beyond or vanished from the study site. Clearly, this pavement enhances secondary wind dispersal, which is supported by the observation of samaras rolling over this type of surface, but ending their observed travel in adjacent habitats. In contrast, the morphological irregularities of the other pavement type slow down or even halt secondary dispersal processes.

During the observation period, 17% of exposed samaras accumulated in patches with sparse vegetation and a planted tree in the middle (Table 4). Almost all of them were recaptured there repeatedly, which indicates that their travels terminated there. Studies on the habitat association of *Ailanthus* in cities illustrate that patches with planted trees embedded in the pavement and usually extending along roads are suitable as safe sites for germination and seedling establishment (Lenzin et al. 2001). Due to the rapid juvenile stem elongation, young saplings can even compete with planted trees (I. Kowarik, personal observation). One-year-old seedlings can reach 1–2 m tall (Hu 1979), and 2-year-old seedlings on an urban site developed shoots up to 1.72 m with an average shoot length of 0.82 m, which clearly exceeded those of other tree species (Pan and Bassuk 1986).

As germination occurs easily on bare soil (Kostel-Hughes et al. 2005), pavements with large joints, and analogously cracks and crevices in asphalt and concrete surfaces, are also suitable for germination and seedling establishment. Within a city block in Ithaca, New York, *Ailanthus* was relatively more frequent on sites with limited topsoil than in other habitats (Pan and Bassuk 1986), and 20% of mapped individuals in Basel, Switzerland, had colonized cracks and crevices (Lenzin et al. 2001). *Ailanthus* also tolerates drought, salt, and herbicide application, frequently occurring stressors along transport corridors (Kowarik and Säumel 2007). We thus conclude that secondary wind dispersal provides access to a range of safe sites in urban road corridors—and this certainly also holds for the road system outside of cities as shown by the colonization of an array of open or disturbed road sites by *Ailanthus* (e.g., Huebner 2003; Merriam 2003; Hulme 2004). Some studies have illustrated that such populations can function as foci for the invasion of adjacent habitats such as agricultural fields, meadows, vineyards, and old fields (Kowarik 1983; Facelli and Pickett 1991; Huebner 2003), but, to our knowledge, seed movement from road corridors to adjacent habitats has not been directly measured thus far.

### ***Possible interaction with other dispersal vectors***

The tail of a dispersal kernel is of significant ecological and evolutionary importance but is usually hard to capture (Williamson 2002; Soons and Ozinga 2005). As almost two-thirds of the exposed samaras vanished during the observation period, we were not able to track the tail of the dispersal kernel although we searched the road corridor and visibly accessible open spaces far beyond the study site as carefully as possible. It thus remains an open question whether the missing samaras were moved and crushed in the



traffic or if some were lifted by vertical turbulence and then transported away from the road corridor, possibly by way of the local wind field.

The recapture of 10% of the exposed samaras at the edge of the traffic lane illustrates that some of the samaras can be moved from the sidewalk to the traffic lanes. Here, interactions between secondary wind dispersal and traffic-induced dispersal may occur and could increase the achieved transport distances. Vehicles have been shown to move samaras like that of *Ailanthus* over long distances (von der Lippe and Kowarik 2007a), and samaras can also be moved by the wind slip of passing vehicles (von der Lippe et al., unpubl.). As the traffic speed was low in our study area (< 50 km/h), and a lane with parked cars acted as a buffer between the moving traffic and the sidewalk area we assume a negligible influence of passing vehicles on the observed dispersal processes along the sidewalk. This idea is supported by results from another experiment on the movement of samaras in the wind slip of passing vehicles. In this case, samaras that were released on the shoulder of the road were scarcely moved, in contrast to those released in the lanes of traffic (von der Lippe et al., unpubl.).

Hence, our experiment illustrates the functioning of secondary wind dispersal as a traffic-independent driver of LDD in transportation corridors. Yet the unclear fate of the vanished diaspores in our experiment illustrates that this mechanism is one part of a multi-vector dispersal process along roads.

## Conclusions

Our results suggest that impervious surfaces within road corridors can function as powerful avenues of secondary wind dispersal. Propagules of species with morphological adaptations to wind can be moved over long distances along roads even without interference of traffic. This vector thus offers a functional explanation for the invasion success of *Ailanthus* at isolated patchy urban sites. Our results suggest that the presence of such sites within the network of impervious surfaces such as asphalt, concrete or other types of pavement may enhance connectivity for species with adaptations to secondary wind dispersal such as *Ailanthus*. Yet it remains a challenge to test whether our results can be generalized for other species and how morphological variation of propagules of a larger species set as well as differences in urban surfaces relate to the vector strength.

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## Counting “exotics”

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An introduced or exotic species is commonly defined as an organism accidentally or intentionally introduced to a new location by human activity (Williamson 1996; Richardson et al. 2000; Guo and Ricklefs 2010). However, the counting of exotics is often inconsistent. For example, in the US, previously published plant richness data for each state are only those either native or exotic to the US (USDA and NRCS 2004), not actually to the state. Yet, within-country (e.g., among states, counties) species introductions which form “homegrown exotics” (Cox 1999) or “native invaders” (Simberloff 2011) are undoubtedly numerous. The growing human population and associated activity increase species introductions at all levels, both international and internal but to date intercontinental species introductions have always been the focus. Those species introduced among neighboring areas are often unnoticed but they are actually far more frequent due to the proximity and environmental similarities. Many domestic exotic plant species exhibit high invasiveness such as *Spartina alterniflora* (smooth cordgrass; introduced from the east coast to California) and *Molothrus ater* (brown-headed cowbird; introduced from the Great Plains to California).

How widespread is the mismatch between definition and practice? It varies among countries and taxonomic groups. Based on the published records of plant introductions, virtually all the large countries in the world such as China, Canada, Russia, India, Australia, and the United States have not included domestic exotics in counting exotic richness in internal units (e.g., states, provinces, counties; but see Kartesz 2010).

In other words, the national boundaries are used to count exotics. This is because, for many taxonomic groups, species introductions among internal administrative units are rarely monitored. The effect of using national boundary to count exotic species becomes greater when the internal units become smaller. For example, within California, detailed records show many native species (to some parts of the state) have been naturalized in other parts of the state (e.g., Hickman 1993; S. Norman, pers. commun.). In contrast, as the focal area becomes larger, the exotic species pool becomes smaller (at the global scale, there are no exotic species).

Using boundaries larger than the concerned internal units could drastically underestimate the exotic richness (and overestimate native species richness). The native species richness automatically changes when the “exotic” species richness has been correctly estimated. After the correction is done, it is critical to re-examine and evaluate previously reported diversity patterns, the relationships between the natives and exotics, and the relationships of species richness in different categories with other biotic, social, and physical variables.

Also, there are discrepancies in domestic species introductions among taxonomic groups. For example, domestic species introduction of fishes within the US but among drainages (not states) usually have good records (e.g., Fuller et al. 1999). Therefore, comparing invasion patterns for different groups needs to take this into account.

In short, counting exotics correctly is critical in invasion biology, conservation, and biogeography. Similar to international species invasions, internal species introductions also have serious ecological and environmental consequences thus pose significant social-economic problems (Cox 1999). For example, as with foreign exotics (Lockwood and McKinney 2001), internal species introductions also homogenize local, state, and national floras and thus lead to similar ecological/social consequences. Indeed, internal species introductions apparently have a greater homogenizing effect than external introductions for plants and fishes (McKinney 2005) and mammals (Spear and Chown 2008).

To provide quality information for more effective management, close monitoring of internal species introductions among states (or provinces especially in large countries) is urgently needed. Public education and policy/management decisions should be in place. Domestic species introductions, for whatever reason (e.g., market-based trade and travel or accidental), should be minimized, especially if some of the species may be highly invasive. Other actions may include: (1) checking local seed/plant companies and nurseries regarding their sources, (2) monitoring major transportation ports/hubs, and (3) using truly local species (not those native only to the US but those native to the immediate vicinity) for restoration. At present, such practice and/or regulations either do not exist or are minimal. Indeed, identifying species introduced across states or provincial borders is challenging as we need to separate them from natural migrants (not “exotics” by definition) for various reasons. However, because of the proximity and unprecedented and increasing within-country traffic, human induced species introductions should be reduced to the minimum level possible.



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