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ORIGINAL PAPER

Historical anthropogenic disturbances influence patterns of non-native earthworm and plant invasions in a temperate primary forest

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Abstract Time lags are of potentially great importance during biological invasions. For example, significant delays can occur between the human activities permitting the arrival of an invader, the establishment of this new species, and the manifestation of its impacts. In this context, to assess the influence of anthropogenic disturbances, it may become necessary to include a historical perspective. In this study, we reconstructed the history of human activities in a temperate forest now protected as a nature reserve to evaluate the magnitude and duration of the impact of human disturbances (e.g. trails, old quarries), as well as environmental factors, in explaining the probability of occurrence and the intensity of invasion by non-native earthworms and plants. The present-day patterns of distribution and intensity of earthworms and plants were better explained by proximity to the oldest human disturbances (initiated more than a century ago) than by proximity to more recent disturbances or to all disturbances combined. We conclude that understanding present-day patterns of non-native species invasions may often require reconstructing the history of human disturbances that occurred decades or even centuries in the past.

Keywords Human activities · Ecological legacies · Nature reserve · Lumbricidae · *Taraxacum officinalis* · Historical ecology · Time lag

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Introduction

In the absence of long-term data, slow ecological changes can remain "invisible" to researchers, and transient phenomena occurring over decades or centuries can be impossible to fully understand (Magnuson 1990; Vellend et al. 2013). Due to the potential for extended time lags between habitat disturbance and species responses, revealing the influence of human activities on the invasion process can be difficult without adopting a historical approach (Flinn and Vellend 2005; Josefsson et al. 2009; Jackson and Sax

2010; Piqueray et al. 2011). Some important drivers of ecological changes can show substantial delays prior to measurable impacts on the ecosystem (Foster 2000). For example, there may be significant time delays between the arrival of an invasive species, the establishment of reproductive individuals and the manifestation of impacts on native communities (Crooks 2005).

Large mature temperate forests appear relatively resistant to biological invasions (Martin and Marks 2006; Essl et al. 2012). Interiors of large forest fragments have been found to be relatively weakly affected by non-native plant invasions, and occurrence of non-native plants is often limited to the edges (Theoharides and Dukes 2007; Fridley 2011; Koncz et al. 2011). Several forest characteristics have been suggested to explain this apparent invasion resistance: a dense canopy (reducing light availability), the thickness of leaf litter (acting as physical barrier to seedling establishment), and the biological inertia due to very long lifespans of the dominant species (Brothers and Spingarn 1992; Von Holle et al. 2003; Bartuszevige et al. 2007; Martin et al. 2009; Vallet et al. 2010). In short, the seemingly high resistance to invasion of mature temperate forests may be due simply to particularly long time lags in relation to human life spans, with disturbances ultimately expected to facilitate invasion (Martin et al. 2009).

The invasibility of forest interiors by non-native plants has been shown to be increased by anthropogenic disturbances, which result in the introduction and dispersal of seeds as well as habitat modification that increases establishment success (Hobbs and Huenneke 1992; Gavier-Pizarro et al. 2010). At the landscape scale, distance from roads and other human disturbances are often good predictors of non-native plant richness and can significantly increase the spread and establishment of non-native plants inside protected areas (Jodoin et al. 2008; Lilley and Vellend 2009; Meunier and Lavoie 2012; Pollnac et al. 2012). This process may span decades, with substantial time lags occurring, especially when habitat suitability is relatively low (Jackson and Sax 2010; Bennett et al. 2013). At our study site, the Gault Nature Reserve, Gilbert and Lechowicz (2005) found no relationship between exotic species richness and distance from present-day human disturbances (trails, reserve perimeter). However, they did not incorporate information on historical disturbances into their study and may therefore have failed to detect disturbance effects given the potential for long time lags in biotic responses.

In historically earthworm-free forests of eastern North America, invasion of European earthworms has been shown to be strongly related to human activities, which result in the introduction of propagules in new locations where subsequent establishment and spread will depend on habitat suitability (Kalisz and Dotson 1989; Suarez et al. 2006; Tiunov et al. 2006; Cameron et al. 2007). Forest interiors appear to be relatively unaffected by earthworm invasion: the probability of earthworm occurrence and the extent of spread increases as a function of proximity to roads and developments (Cameron and Bayne 2009; Sackett et al. 2012; Shartell et al. 2013). Invasion of non-native species in the family Lumbricidae tend to advance across forested landscapes in sequential waves, with epigeic species (those living in leaf litter) followed by endogeics (those living in the soil) and then anecics (those making deep vertical tunnels), with the impacts on plant communities increasing as this succession proceeds (James and Hendrix 2004; Hale et al. 2005; Holdsworth et al. 2007; Addison 2009). This sequence of invasions could be explained in part by greater reproductive capacities, colonization rates and environmental tolerance limits of the pioneer species in comparison with the later arrivals (Holdsworth et al. 2007). It has also been suggested that by altering the intact forest floor, by mixing O and mineral soil horizons, and by increasing the soil pH, the first acid-tolerant litter-dwelling (epigeic) invaders such as *Dendrobaena octaedra* and *Lumbricus rubellus* may facilitate the invasion of endogeic and anecic species, which are thought to be less acidophilic and less capable of establishing on intact forest floors (Hale et al. 2005; Suarez et al. 2006; Tiunov et al. 2006; Addison 2009). In either case, time lags of multiple decades have been hypothesized to occur between the beginning of earthworm invasion in a local area and the development of a complex assemblage of different ecological groups including endogeic and anecic species (Hale et al. 2005; Tiunov et al. 2006; Stoscheck et al. 2012). However, few studies have taken a long-term perspective on the timing and rate of earthworm invasion at specific sites (see Larson et al. 2010).

The co-occurrence of relatively high abundances of non-native earthworms and non-native plants has been observed in many temperate forests of north-eastern

North America (e.g. Kourtev et al. 1999; Nuzzo et al. 2009). This could be explained by the fact that both taxa thrive on soils with thin leaf litter and relatively high pH (Kourtev et al. 1999; Heimpel et al. 2010) and have similar human-mediated modes of dispersal. Alternatively, facilitation of non-native plant invasions by the prior establishment of endogeic and anecic earthworms has been proposed as an example of "invasional meltdown": a process by which one group of non-native species facilitates invasion by another group (Simberloff and von Holle 1999; Simberloff 2006; Heimpel et al. 2010). Endogeic and anecic earthworms could facilitate the colonization of non-native plants by creating soils with thin litter and elevated pH and nitrate availability (Kourtev et al. 1999; Nuzzo et al. 2009; Belote and Jones 2009; Heimpel et al. 2010). Introduction of large European earthworms into earthworm-free forests might also be an important driver of declines of native plants, thereby reducing competition for non-native invaders (Bohlen et al. 2004; Frelich et al. 2006; Sutherland et al. 2011).

Although the influence of human activities in heavily disturbed ecosystems is well demonstrated, fewer studies have investigated more subtle human influences in relatively pristine forest ecosystems (Josefsson et al. 2009). In addition, while it has been suggested that the ability to predict the intensity of earthworm invasions may be improved by taking into account not only the presence of anthropogenic disturbances but also their duration (Hale et al. 2005; Tiunov et al. 2006), only a few studies have tested this hypothesis (see Cameron and Bayne 2009; Sackett et al. 2012). The goal of the present study was to test if recent and historical (initiated >100 years ago) anthropogenic disturbances had different effects on present-day patterns of non-native plants and earthworms in a large, mature temperate forest. Specifically, we assessed (1) the relative importance of proximity to human disturbances occurring at different times in the past and of physical environmental conditions in predicting the pattern of non-native earthworm invasions, and (2) the relative importance of these same variables as well as properties of the earthworm community in predicting the pattern of non-native plant invasions. To address these questions, we reconstructed as accurately as possible the history of human disturbances inside and around our study site, the Gault Nature Reserve (Mont St.Hilaire, Qc, Canada). We predicted that because the dispersal of both earthworms and plants are often linked to human activities, the occurrence and intensity of earthworm invasion and the establishment of non-native plants would be greatest in areas close to the oldest human activities, regardless of whether those activities are ongoing in the present-day landscape. We also predicted that non-native plant establishment would be correlated with the intensity of earthworm invasion.

Methods

Study area

This study was undertaken in the 10-km^2 Gault Nature Reserve (www.mcgill.ca/gault), which is located on one of the Monteregian hills (Mont St-Hilaire) 35 km east of Montreal, Quebec, Canada (45°32′N, 73°08′W). The reserve, which is surrounded by agricultural and suburban development, protects a primary forest dominated by *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech) and *Quercus rubra* (red oak) (Gilbert and Lechowicz 2005). The site has experienced highly localized anthropogenic disturbances since Europeans first settled the region in the eighteenth century.

History of human activities in the Gault Nature Reserve

The influence of people of European origin on Mont St-Hilaire and the surrounding area began around 1745 with establishment of the "Village de la Montagne" on the southern flanks of the mountain centered along the millstream draining Lake Hertel (see Online Resource 1 for supporting references). Construction of a "Chemin de la Montagne" (a road) in 1768 accelerated conversion of the lower southern slopes to farmland. By 1850, the area had about 1,500 inhabitants, nine mills, three tanneries, two forges, a foundry and a distillery. Exploitation of natural resources had increased with the construction of two lime kilns and a proliferation of sugar shacks in the Lake Hertel basin on Mont St-Hilaire. Two major trails were established in this era, one a backfilled trail used to transport the limestone quarried on the northeastern flank of the mountain to the village and the other a much used “Way of the Cross” ascending from the village to a chapel and 30-m high cross erected on the highest peak on Mont St-Hilaire. A railway completed in 1848 increased access to the region and tourist facilities (a café, a 125-room hotel) were built around the village and on the shores of Lake Hertel in the second half of the nineteenth century. In the early twentieth century, intrusive use of Mont St-Hilaire declined with destruction of the on-site hotel by fire, local abandonment of maple sugar production, and the increasing obsolescence of water-powered mills.

The economic downturn in the early twentieth century created an opportunity that led to the protection of Mont St-Hilaire. In 1913, Andrew Gault purchased 890 ha on Mont St-Hilaire from the Campbell family with the intention of using the property as a private forest reserve. He significantly reduced exploitation of the forest but continued to allow local people to fish in Lake Hertel and maintained a small orchard. In 1958, Gault bequeathed his property to McGill University with the restriction “…that its beauties and amenities may be preserved for all time to come”. The university expanded protection efforts: cutting the orchard in the reserve in 1960; designating a conservation area closed to the public in 1968; creating the Mont St-Hilaire Nature Conservation Centre (www.centrenature.qc.ca/) in 1972; and acquiring adjacent properties to enlarge the reserve. During the second half of the twentieth century, the protected status of the reserve was strengthened by designation as a federal migratory bird sanctuary in 1960, as the first Canadian UNESCO Biosphere Reserve in 1978 and as a Nature Reserve on Private Land under Québec law in 2004. Several anthropogenic pressures nonetheless persist at the site including increasing residential development at the western side of the reserve and a steadily increasing number of visitors using a trail network that has expanded since the 1960s.

Site selection

In 2002, Gilbert and Lechowicz (2004) established 69 permanent vegetation plots distributed to ensure spatial and environmental representation and minimal correlation between distance and environmental similarity; to better assess near-distance effects 16 additional plots were added in 2004 within 100 m of existing ones. Only forest sites not visually affected by ongoing human activities were chosen; areas within 15 m of the outer perimeter of the reserve or within 10 m of a trail or the shore of Lake Hertel were excluded. These 85 plots were used in the present study (Fig. 1).

Plant and earthworm surveys

We surveyed the understory herbaceous layer and earthworm communities at each of the 85 plots. From 6 May to 8 August 2011—during three separate visits—percent cover of all vascular plants <1.5 m tall was estimated in 50-m^2 circular plots centered on a permanent marker (Gilbert and Lechowicz 2004). Nomenclature and species origins (native or non-native) follow Brouillet et al. (2010) and Lavoie et al. (2012). *Poa* species, which in vegetative condition can only be identified to the genus level, were excluded from our analyses because both native and non-native *Poa* occur on Mont St-Hilaire. With this exception we focused on the distributions and diversity of the non-native plants in the 85 study plots to draw comparisons with the factors influencing non-native earthworms.

In May 2012, we collected earthworms in four 25 cm × 25 cm quadrats at all 85 plots, with one quadrat in each cardinal direction at a distance of 5 m from the permanent marker; at three sites, only 2–3 quadrats were sampled due to a lack of unsaturated soils (total number of quadrats = 336). We used the liquid-mustard extraction technique, which provides a consistent estimation of the presence and relative abundance of earthworms across a range of soils (Wironen and Moore 2006; Valckx et al. 2011; NRRI 2011). Leaf litter was first removed from the quadrat and manually sorted to search for errant earthworms. Subsequently, over a period of 20 min, two liters of 10 g/L mixture of commercial dry mustard in water was poured on the soil surface in two applications and all emerging earthworms were collected and preserved in a 70 % isopropyl alcohol solution. Earthworms were identified to species (genus for the juveniles) using the key from Reynolds (1977) and uncertain individuals were sent to Dr. J.W. Reynolds of the Oligochaetology Laboratory (Kitchener, Canada) for identification.

Historical and environmental data collection

The ages and locations of human disturbances were determined using historical maps and publications

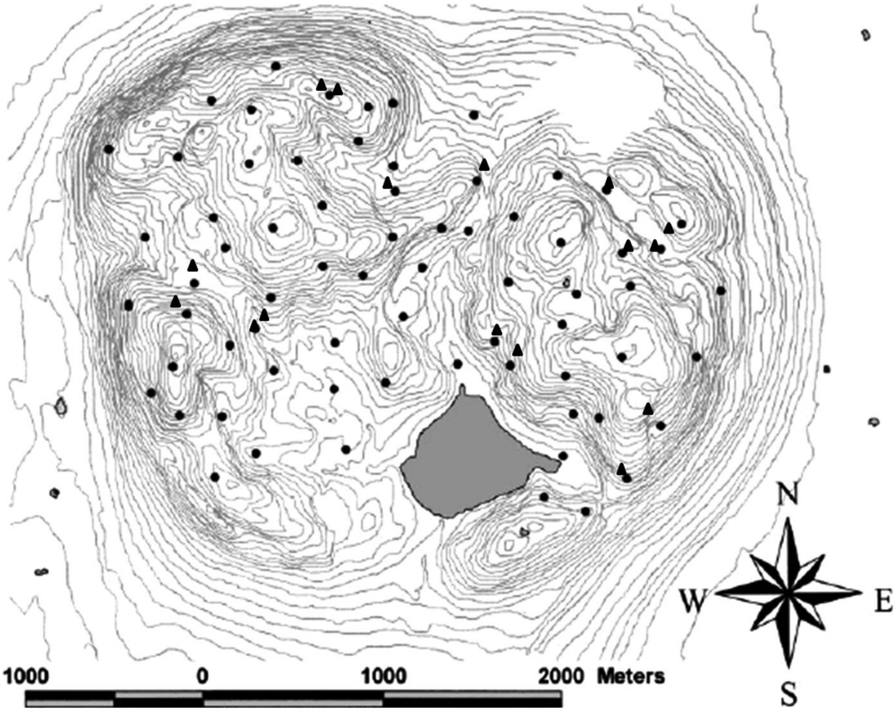

Fig. 1 Spatial distribution of sampling points. *Contours* are at 10-m intervals, for a total elevational gradient of 230 m over the area sampled. Map modified from Gilbert and Lechowicz (2004) (*triangles* represent the 16 sites added in 2004)

(Fig. 2; Online Resources 1 and 2). For analysis, disturbances were divided into those initiated either during two time periods (before and after 1910) or during four time periods (before 1845; 1846–1910; 1911–1969 and after 1969). These divisions were established to provide periods of roughly 100 or 50 years, respectively. For each site, the distance from the nearest disturbance in each category was calculated using overlays of site positions and disturbance locations in a Geographical Information System (ESRI© ArcGIS 10.0). Analyses using either two or four categories of historical disturbance yielded essentially the same results. We present only the results using two time periods: before and after 1910 (Online Resources 3 and 4 shows the results using the separation into four periods of time).

Based on the predictors of earthworm and non-native plant invasions found in previous studies, we measured environmental variables potentially influencing the establishment of non-native earthworms and plants at the same 85 sites. We measured soil pH, presence/absence of leaf litter, slope steepness, elevation, an index of leaf litter palatability (described below) and distance from permanently wet habitats as factors relevant to earthworm invasion (Suarez et al. 2006; Tiunov et al. 2006; Wironen and Moore 2006; Shartell et al. 2013) and soil pH and moisture, slope steepness, elevation, presence/absence of leaf litter and canopy closure as factors relevant to non-native plant invasion (Rejmanek 1989; Gilbert and Lechowicz 2005; Fridley 2011; Pollnac et al. 2012). Since many authors (Kourtev et al. 1999; Nuzzo et al. 2009; Heimpel et al. 2010; Eisenhauer et al. 2012) have suggested that the presence of endogeic or anecic earthworms could favor the establishment of non-native plants, we also used this binary variable (presence/absence of earthworm invasion stage 2, described below) as a potential predictor of non-native plant invasions.

Soil pH was measured on four pooled soil cores taken in July 2012 to a depth of 8 cm. To provide an index of the palatability of litter to earthworms, in 50-m^2 circular plots, we estimated percent cover of each tree species for the stratum >3 m and took the sum across the following species recognized to have highly palatable leaves due to high calcium content: *A. saccharum*, *F. americana*, *Tilia americana* and *Alnus rugosa* (Hendriksen 1990; Reich et al. 2005; Tiunov et al. 2006). Distance from refugia favoring earthworm survival during drought was calculated using

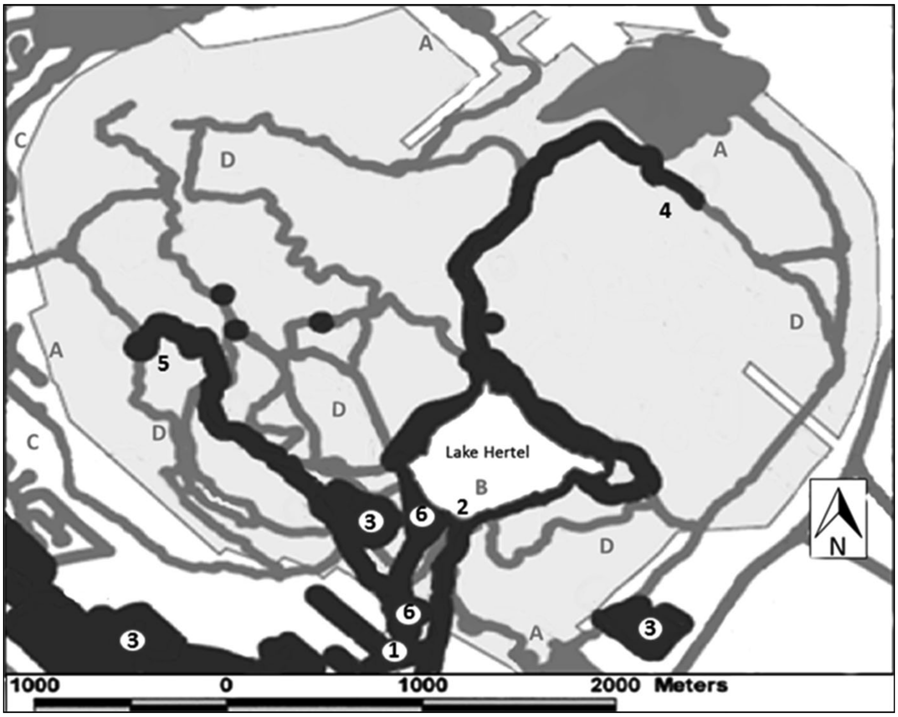

Fig. 2 Locations of the principal anthropogenic disturbances occurring inside or around the Gault Nature Reserve (whose current territory is represented in *pale gray*). Historical disturbances (in *black*) are: *1* a millstream village and *2* associated dam originating in the late eighteenth century; *3* orchards; *4* a nineteenth century lime kiln and associated backfilled trail; *5* the nineteenth century cross and associated trail, and *6* a nineteenth century hotel and café. Twentieth century disturbances (in *dark gray*) are: *A* quarries and sand pits; *B* fishing in Lake Hertel; *C* residential development and *D* the expansion of the trail network

GIS overlays of site positions and hydrological conditions (streams, lakes, ponds) (ESRI© ArcGIS 10.0). Soil moisture in the plots was estimated from the mean of three measurements taken in July 2012 to a depth of 5 cm using a Delta-T Devices theta probe (type ML2x, Cambridge, UK). The presence of leaf litter was scored at each site in May 2012 as a binary variable: presence (regardless of thickness) or absence (bare soil). Finally, we used the Gap Light Analyzer software (Frazer et al. 2000) with hemispherical canopy photographs taken 1 m above the ground in July and August 2011 at the plot center to determine canopy openness.

Analyses

We quantified earthworm and plant invasions in two ways, intensity and occurrence. To characterize the intensity of earthworm invasion, sites were classified into three stages according to the presence of species or ecological groups indicative of the successional sequence typical of earthworm invasions in north-eastern American forests: 0 = earthworm-free; 1 = only epigeic or epi-endogeic species (*Dendrobaena* spp., *Lumbricus rubellus*); and 2 = presence of endogeic or anecic species (*Aporrectodea* spp., *L. terrestris*) (Addison 2009; Hale et al. 2005; Holdsworth et al. 2007). To reflect the intensity of non-native plant establishment, sites were classified into three stages according to the number of non-native species established: 0 = none; 1 = one species; and 2 = two or more species (the maximum was four species). Occurrence (i.e., presence vs. absence) was analyzed for several groups of interest of earthworms (epigeic or epi-endogeic species, endogeic or anecic species, and any non-native earthworms) and of non-native plants (the two main species, *Epipactis helleborine* and *Taraxacum officinale*, and any non-native plant species).

All analyses were conducted in R version 2.14.1. We used binomial logistic regressions (clm{ordinal}, Christensen 2012) to evaluate the ability of distance to disturbances within each time period to explain the occurrence of non-native plants and earthworms. Ordinal logistic regressions were used to predict the intensity of earthworm or plant invasion (Guisan and Harrell 2000; Jodoin et al. 2008; Meunier and Lavoie 2012). The importance of distance to disturbances during the different time periods was assessed by model ranking based on the Akaike information criterion. Each candidate model included distance to disturbance in a given

Table 1 Occurrence, maximum and mean density and maximum and mean biomass of non-native earthworms

Species	No. plots occupied	Maximum density (# m^{-2})	Mean density (# m^{-2}) ± SD	Maximum biomass (g m^{-2})	Mean biomass (# m^{-2}) ± SD
Immature *Aporrectodea*	17	380	70.4 ± 94.1	2.58	0.71 ± 0.76
Aporrectodea rosea	4	112	60.3 ± 33.4	1.05	0.69 ± 0.28
Aporrectodea trapezoides	13	68	23.1 ± 19.9	3.73	1.49 ± 1.13
Dendrobaena octaedra	33	100	23.0 ± 20.4	1.11	0.18 ± 0.20
Dendrobaena rubida	4	24	10.0 ± 8.3	0.32	0.14 ± 0.12
Eiseniella tetraedra	3	21	9.8 ± 8.2	0.06	0.04 ± 0.02
Immature *Lumbricus*	13	60	25.4 ± 17.1	1.21	0.50 ± 0.40
Lumbricus rubellus	6	4	4.0 ± 0.0	0.49	0.31 ± 0.17
Lumbricus terrestris	11	16	9.3. ± 4.5	9.83	3.44 ± 2.72

Earthworm biomass (ash-free dry mass) was estimated using length measurements and the general allometric equation of Hale (2004). Note that mean ± SD are only for the subset of plots where the species in question was present

SD standard deviation

time period, with all models including the environmental variables listed above (aictab{AICcmodavg}, Mazerolle 2013). For the model with the highest statistical support, Wald tests in multiple regression were used to evaluate the significance of a given proximity-to-disturbance variable and its relative importance in comparison to the environmental variables (lrm{rms}, Harrell 2013). Multicollinearity was tested using the variance inflation factor (VIF), with all VIF <3 (Dormann et al. 2013). Assumptions about ordinality and proportional odds were verified using plot.smean.ordinality{rms} and the goodness of fit was tested using residuals.lrm{rms} (Harrell et al. 1998; Guisan and Harrell 2000).

Results

A total of seven different non-native earthworm species and 13 non-native plant species occurred in our plots (Tables 1, 2). All are of European origin. Non-native earthworms were found in 60 % of the surveyed plots, with species richness ranging from 0 to 4 (median = 1). Forty percent of the plots showed the presence of only epigeic or epi-endogeic species (*Dendrobaena* spp., *Lumbricus rubellus*), and 26 % of the plots showed endogeic or anecic species (*Aporrectodea* spp., *Lumbricus terrestris*). Non-native plants were present in 75 % of the surveyed plots, with species richness ranging from 0 to 4 (median 1). Only two non-native species were frequent: *Epipactis helleborine* in 46 % of the plots and *Taraxacum officinalis* in 54 %. No non-native plants were dominant in any plot; their cover never exceeded 1 %.

The occurrence of epigeic or epi-endogeic earthworm species (*Dendrobaena* spp., *Lumbricus rubellus*; Table 3a) was best predicted by the model including distance from any human disturbance; this model had an Akaike weight (Wi) of 0.84 (Wi = the probability that this model is the best among all candidate models). In this model, proximity to any human disturbance was the best predictor ($P = 0.0072$), although elevation was also significant (Table 4a; Fig. 3a). In contrast, for the occurrence of endogeic or anecic earthworm species (Table 3b), the model including distance to historical (pre-1910) human disturbances received the strongest support (Wi 0.94). In this model, the most significant variable was proximity to historical human disturbances (Table 4b, $P = 0.0068$; Fig. 3b). Only one environmental variable was also significant: the absence of leaf litter. Similarly, for all earthworm species combined (Table 3c, d), models including

Table 2 Occurrence and cover of non-native plants

Species	No. plots occupied	Maximum cover in any plot (%)	Mean cover (%) ± SD
Achillea millefolium	2	0.1	0.1 ± 0
Arctium lappa	1	0.1	0.1 ± 0
Barbarea vulgaris	1	0.1	0.1 ± 0
Chenopodium album	1	0.1	0.1 ± 0
Dactylis glomerata	1	0.25	0.25 ± 0
Epipactis helleborine	39	0.25	0.13 ± 0.06
Galeopsis tetrahit	1	0.5	0.5 ± 0
Geranium robertianum	3	0.25	0.2 ± 0.07
Oxalis stricta	3	0.25	0.15 ± 0.07
Taraxacum officinalis	46	1	0.12 ± 0.13
Trifolium pretense	1	0.1	0.1 ± 0
Tussilago farfara	1	0.25	0.25 ± 0
Valeriana officinalis	2	0.25	0.18 ± 0.08

Note that the mean ± SD is only for the subset of plots where the species in question was present

SD standard deviation

Table 3 Results of multiple logistic regression models used to evaluate the relative importance of the distance from historical, recent and all human disturbances in comparison to environmental variables alone in predicting the occurrence of (a) epigeic or epi-endogeic earthworms; (b) endogeic or anecic earthworms; (c) all earthworm species and (d) the intensity of earthworm invasion in the Gault Nature Reserve (Quebec, Canada)

Models	AIC_c	Δi	*Wi*
(a) Occurrence of epigeic or epi-endogeic earthworms			
Distance from historical disturbances + ENV	121.58	5.78	0.05
Distance from recent disturbances + ENV	120.41	4.61	0.08
Distance from all disturbances + ENV	115.80	0.00	0.84
ENV	122.48	6.68	0.03
(b) Occurrence of endogeic or anecic earthworms			
Distance from historical disturbances + ENV	72.54	0.00	0.94
Distance from recent disturbances + ENV	79.77	7.23	0.03
Distance from all disturbances + ENV	82.39	9.85	0.01
ENV	79.97	7.42	0.02
(c) Occurrence of any non-native earthworms			
Distance from historical disturbances + ENV	104.74	0.00	0.88
Distance from recent disturbances + ENV	111.81	7.08	0.03
Distance from all disturbances + ENV	111.44	6.70	0.03
ENV	109.85	5.11	0.07
(d) Intensity of earthworm invasion			
Distance from historical disturbances + ENV	160.79	0.00	0.98
Distance from recent disturbances + ENV	171.51	10.72	0.00
Distance from all disturbances + ENV	171.60	10.81	0.00
ENV	169.97	9.18	0.01

The second-order Akaike Information Criterion (AICc), the delta AIC (Δi) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and Δi < 2) are in bold. ENV represents the set of environmental variables used for either earthworms or plants (described in the "Methods")

distance to historical human disturbances received the most support in predicting both the occurrence of invasion (Wi 0.88) and the intensity of invasion (Wi 0.98). For both response variables, the significant explanatory variables in the best model were the proximity to historical human disturbances, slope steepness and the absence of leaf litter (Table 4c, d; Fig. 4; Online Resource 5).

For non-native plants, no model convincingly (i.e., with Wi >0.80) explained either the occurrence of *E. helleborine* or the occurrence of at least one non-native plant species (Table 5a, c). In contrast, the model including distance to historical human disturbances explained the distribution of *T. officinale* with substantial support (Wi 0.91; Table 5b). In this model, the proximity to historical human disturbances, elevation and the presence of earthworm invasion stage 2 were significant predictors (Table 6b; Online Resource 6). For the intensity of non-native plant invasion, the best model included proximity to historical human disturbances (Wi 0.91; Table 5d,). In this

Table 4 Significant ($P < 0.05$) explanatory variables in the best models from Table 1

Significant explanatory variables	β	Z	*P*
(a) Occurrence of epigeic or epi-endogeic earthworms			
Distance from any human disturbances	−0.0073	−2.687	0.0072
Elevation	0.0134	2.026	0.0428
(b) Occurrence of endogeic or anecic earthworms			
Distance from historical human disturbance	−0.0058	−2.704	0.0068
Presence of leaf litter	−2.6239	−2.673	0.0075
(c) Occurrence of any non-native earthworms			
Distance from historical human disturbances	−0.0033	−2.511	0.0120
Presence of leaf litter	−3.4679	−2.404	0.0162
Slope	−0.0229	−2.187	0.0288
(d) Intensity of earthworm invasion			
Presence of leaf litter	−2.8416	−3.571	0.0004
Distance from historical human disturbances	−0.0038	−3.187	0.0014
Slope	−0.0220	−2.355	0.0185

The ordinal regression coefficient beta (β), the Z-value (Z) and the Wald test significance (*P*) are presented for each model

model, the significant explanatory variables were proximity to historical human disturbances and soil pH (Table 6d; Fig. 5).

Discussion

Although significant anthropogenic disturbance undoubtedly has occurred in the Gault Nature Reserve for more than 150 years, non-native earthworms and plants are still absent from parts of the reserve: in 40 and 25 % of our study plots, respectively. While distance from recent disturbances was not a significant predictor of non-native earthworms and plants, distance from human disturbances older than a century was significantly associated with the distribution of both taxa. Only the occurrence of the earthworms in the genus *Dendrobaena* and *Lumbricus rubellus* (characteristic of early successional development in earthworm communities) showed some association with recent disturbance. Our results provide clear evidence that to predict present-day distributions of non-native species it can be important to consider not only the spatial distribution of human disturbance but also the time frame in which the disturbance was prevalent. Some of the oldest disturbances at our study site are scarcely evident in the field at present, yet their influence persists to the present day. Previous research on non-native plants using the same plots (Gilbert and Lechowicz 2005) did not consider this potential impact of proximity to past human disturbances as a factor mediating present day species distributions.

The importance of human disturbances and environmental variables varied among different ecological types of non-native earthworms. Specifically, the epigeic genus *Dendrobaena* (parthenogenic) and the epi-endogeic species *Lumbricus rubellus* were found most often in sites close to any human disturbances (i.e., regardless of age) and at relatively high elevation. In contrast, the endogeic genus *Aporrectodea* and the anecic species *Lumbricus terrestris* were largely restricted to sites closest to the oldest human disturbances and in soils without leaf litter. These

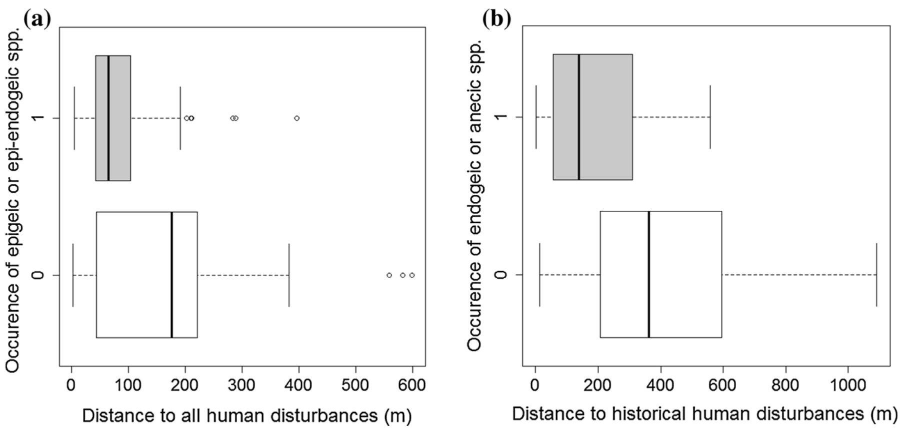

Fig. 3 Occurrence of epigeic or epi-endogeic earthworms (**a**) and occurrence of endogeic or anecic species (**b**) plotted against the most significant explanatory variables (*box plots* of raw data) in the best models predicting these variables. Sites without non-native earthworms are represented in *white*, and sites invaded by non-native earthworms are in *pale gray*

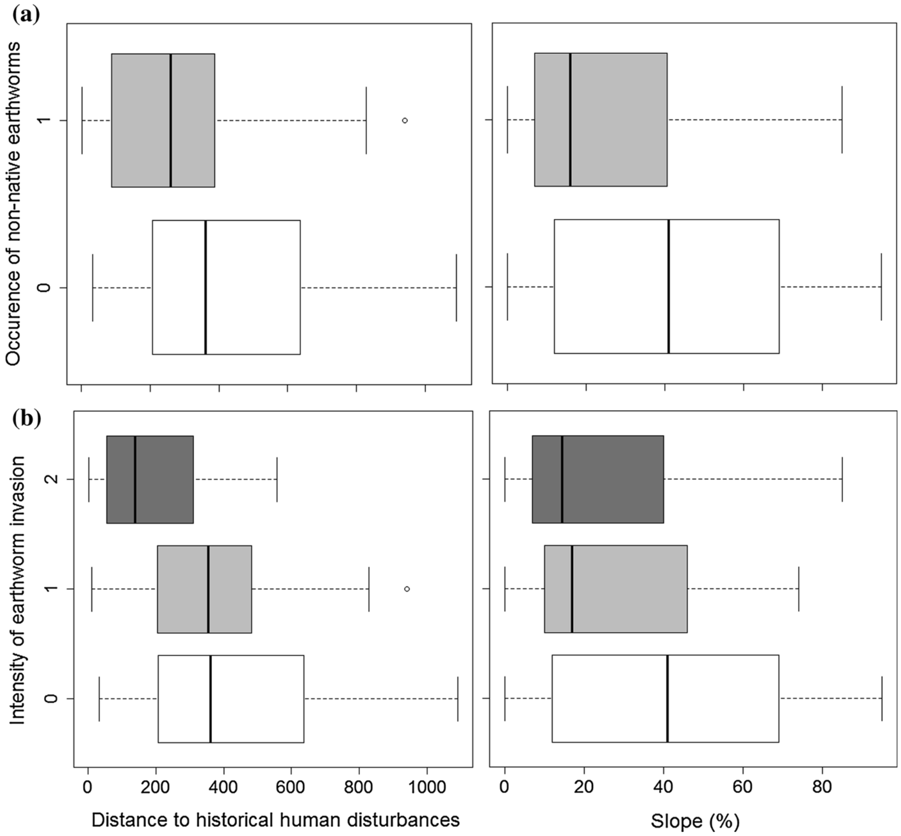

Fig. 4 Occurrence of non-native earthworms (**a**) or the intensity of earthworm invasion (**b**) plotted against the significant variables (*box plots* of raw data) in the best models predicting these variables. For occurrence, sites without non-native earthworms are represented in *white*, and sites invaded by non-native earthworms are in *pale gray*. For intensity, sites in stage 1 (with epigeic species) are in *pale gray*, and sites in stage 2 (with endogeic or anecic species) are in *dark gray*

differences in the predictors of the distributions of ecological types are likely related to differences in species traits. The litter dwelling *Dendrobaena* spp. and *Lumbricus rubellus* are particularly tolerant to drought, cold and acidity and have high cocoon production (Addison 2009; Holdsworth et al. 2007). In addition, *Dendrobaena* spp. are parthenogenic and have smaller cocoons found in the upper leaf litter layers and are therefore particularly likely to be transported by humans and vehicles (Dymond et al. 1997; Cameron and Bayne 2009). All these features allow these worms to have a high colonization rate and thus to quickly establish on sites close to sites of introduction. This could explain why these species have been found in the vicinity of all human disturbances and at sites with well-drained soils at high elevation. In contrast, endogeic and anecic species are thought to have a much lower rate of colonization due to the need for sexual reproduction, lower cocoon production, and more limited environmental tolerance (Butt and Nuutinen 1998; Holdsworth et al. 2007). This could explain why species of *Apporrectodea* and *Lumbricus terrestris* were found only in association with human disturbances older than a century and at sites without thick, acidic leaf litter.

Our results clearly confirm the possibility raised by several authors (Hale et al. 2005; Tiunov et al. 2006; Sackett et al. 2012) that the duration of proximate human activities can be important in predicting the occurrence and intensity of invasion by non-native earthworms. This effect of past anthropogenic disturbances can be crucial for at least two reasons. First, earthworm propagule pressure is inversely related to the distance from sites of earthworm introduction (Holdsworth et al. 2007). For trails and any similar disturbances, the longer the duration of their use, the greater the chances of multiple introductions (Cameron et al. 2008) and the higher the propagule pressure in their surroundings. Second, even if human disturbance increases the invasibility of forest ecosystems in the short term, the spread of exotic species into proximate forest interior may involve extended time lags. For example, in a similar northern hardwood forest, no evidence of range expansion of non-native

Table 5 Results of multiple logistic regression models used to evaluate the relative importance of the distance from historical, recent and all human disturbances in comparison to environmental variables alone in predicting the occurrence of (a) *Epipactis helleborine*; (b) *Taraxacum officinalis*; (c) all non-native plants and (d) the intensity of non-native plant invasion at the Gault Nature Reserve (Quebec, Canada)

Model	AIC$_c$	Δi	*Wi*
(a) Occurrence of *Epipactis helleborine*			
Distance from historical disturbances + ENV	113.87	0.97	0.27
Distance from recent disturbances + ENV	115.01	2.11	0.15
Distance from all disturbances + ENV	115.31	2.41	0.13
ENV	112.90	0.00	0.44
(b) Occurrence of *Taraxacum officinale*			
Distance from historical disturbances + ENV	103.98	0.00	0.91
Distance from recent disturbances + ENV	111.21	7.22	0.02
Distance from all disturbances + ENV	111.89	7.90	0.02
ENV	109.67	5.69	0.05
(c) Occurrence of exotic plants			
Distance from historical disturbances + ENV	91.99	0.00	0.63
Distance from recent disturbances + ENV	96.19	4.20	0.08
Distance from all disturbances + ENV	96.48	4.48	0.07
ENV	94.01	2.02	0.23
(d) Intensity of exotic species richness			
Distance from historical disturbances + ENV	174.57	0.00	0.91
Distance from recent disturbances + ENV	181.30	6.73	0.03
Distance from all disturbances + ENV	181.42	6.85	0.03
ENV	181.42	6.85	0.03

The second-order Akaike Information Criterion (AICc), the delta AIC (Δi) and the Akaike weights (Wi) are presented for each model. Models with substantial evidence (Wi > 0.80 and Δi < 2) are in bold

earthworms was observed at the invasion front over a decade (Stoscheck et al. 2012). According to Hale et al. (2005), it might take several decades before a site reaches a high-intensity invasion status characterized by a complete assemblage of the different ecological types of earthworms.

Table 6 Significant ($P < 0.05$) explanatory variables in the best models from Table 3

Significant explanatory variables	β	Z	*P*
(a) Occurrence of *Epipactis helleborine*			
Soil pH	1.5634	2.421	0.0155
Elevation	−0.0132	−2.196	0.0281
(b) Occurrence of *Taraxacum officinale*			
Elevation	0.0222	2.865	0.0042
Distance from historical human disturbances	−0.0037	−2.645	0.0082
Presence of earthworm invasion stage 2	1.9121	2.108	0.0351
(c) Occurrence of non-native plants			
Soil pH	1.9735	2.265	0.0235
Distance from historical human disturbances	−0.0029	−2.051	0.0402
(d) Intensity of non-native species richness			
Soil pH	1.6478	2.776	0.0055
Distance from historical human disturbances	−0.0026	−2.558	0.0105

The ordinal regression coefficient beta (β), the Z-value (Z) and the Wald test significance (*P*) are presented for each model

For non-native plants, the important predictors of occurrence also depended on the species of interest. The lack of any significant anthropogenic predictor variables for the distribution of *E. helleborine* could be explained by the fact that this generalist orchid, with extremely small and widely dispersed seeds, is well adapted to a variety of sites ranging from shady forests or edges of woodland to a variety of anthropogenic habitats (Kolanowska 2013). Given this broad ecological niche, we would expect a relatively short lag time between its introduction and subsequent spread, and consequently no clear link with the oldest disturbances. In contrast, the distribution of *T. officinalis* was predicted by the proximity to disturbance before 1910. Unlike the individuals of *E. helleborine* observed in the field, which were frequently reproductively mature with flowers and fruits, the individuals of *T. officinale* we encountered in closed forest were almost always non-reproductive, with just a few small leaves. The fact that *T. officinale* is ubiquitous in the seed bank throughout the reserve (Leckie et al. 2000) but not represented by mature individuals could mean that the time required for the establishment of healthy populations has not yet been reached, or that

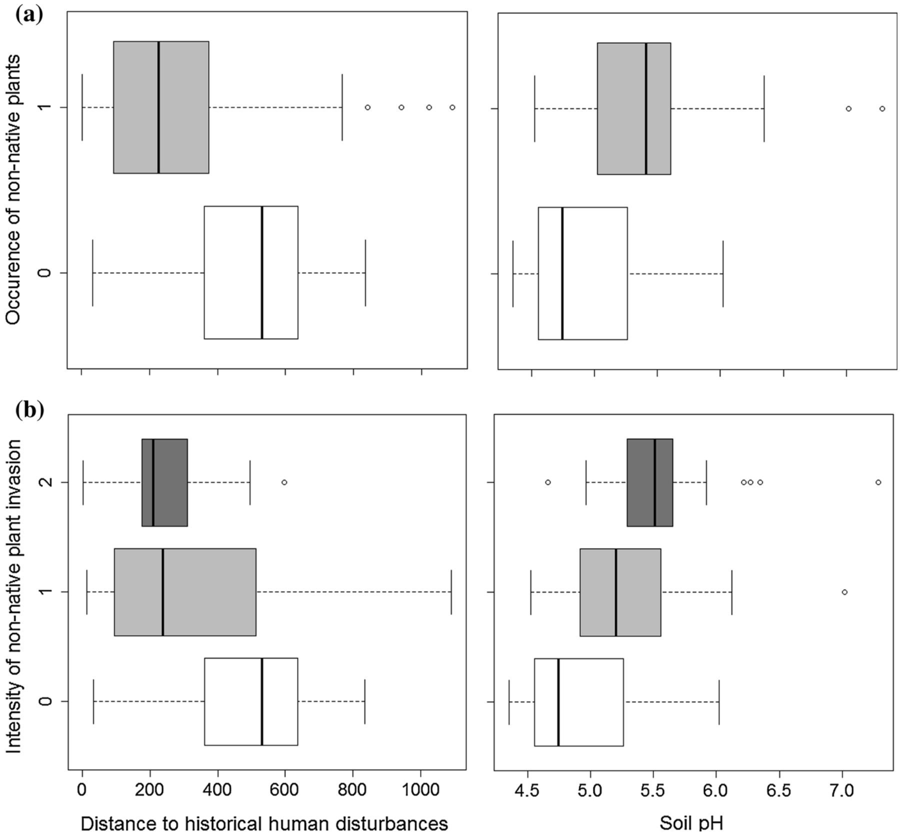

Fig. 5 Occurrence of non-native plants (**a**), and the intensity of non-native plant invasion (**b**) plotted against significant variables (*box plots* of raw data) in the best model predicting these variables. For occurrence, sites without non-native plants are represented in *white*, and sites invaded by non-native plants are in *pale gray*. For intensity, sites in stage 1 (with just one species) are in *pale gray*, and sites in stage 2 (with more than one species) are in *dark gray*

most populations, away from direct disturbance, are demographic sinks.

As predicted, historical disturbance was a strong predictor of the intensity of both non-native earthworm and plant invasions. In addition, a weak positive association was found between endogeic and anecic earthworms and the most common non-native plant *Taraxacum officinalis*. Several hypotheses might explain these results. First, it has been suggested that the factors influencing earthworm invasions are more similar to those influencing plant invasions than to those influencing invasions by more mobile animals, due to reproductive and behavioral features like cocoon/seed production and diapause/seed dormancy (Hendrix et al. 2008). Many non-native earthworms and plants were introduced to North America by similar vectors (e.g. soil dumped from ship's ballast or via imported plants roots) and spread through the landscape has been facilitated by similar human activities (e.g. construction of roads and relocation of fill or horticultural materials) (Hendrix and Bohlen 2002; Bohlen et al. 2004). Secondly, both non-native plants and endogeic or anecic earthworms occupy similar habitat with bare soil and elevated pH (Kourtev et al. 1999; Nuzzo et al. 2009). Leaf litter is often thinner and soil pH often higher at the edge of human disturbances compared to undisturbed forest interiors (Kostel-Hughes et al. 1998; Vallet et al. 2010). Given that the level of human disturbance appears to be correlated with litter depth and pH, both non-native earthworms and plants could be "passengers" taking opportunistic advantage of habitat modification caused by the same human activities (MacDougall and Turkington 2005). However, because these earthworms are able to colonize areas with abundant leaf litter and since soil and litter properties can be directly shaped by invading earthworms, they may also act more importantly as "drivers" of these habitat characteristics. Finally, some have suggested that earthworms could also be drivers of changes in regard to the facilitation of the colonization of non-native plants (Kourtev et al. 1999; Belote and Jones 2009; Heimpel et al. 2010). In fact, endogeic and anecic earthworms are recognized to be important ecosystem engineers that can profoundly alter physico-chemical soil parameters by rapidly removing forest floor materials and by increasing soil pH (Burtelow et al. 1998; Wironen and Moore 2006). Although the presence of endogeic and anecic earthworms does not correlate with non-native plants generally, it does correlate with the most widespread non-native plant species, *Taraxacum officinale*. Our data cannot resolve the causality of the association between non-native earthworms and plants, but the fact that the presence of endogeic and anecic earthworms was a significant predictor of the presence of *T. officinalis* while controlling for environmental variables suggests that these earthworms might be both “passengers” and “drivers” of environmental change.

In conclusion, our results support arguments concerning the importance of accurately reconstructing past human activities in order to fully understand the magnitude and duration of ecological impacts due to anthropogenic disturbances (Flinn and Vellend 2005; Josefsson et al. 2009). Although some historical human disturbance may be unknown or impossible to pinpoint in space or time, and therefore not included in analyses (e.g. minor selective logging far in the past), it appears that our reconstruction captured the key historical disturbances in this ecosystem. Historical disturbances that no longer occur nonetheless seem to have left an important legacy even many decades after these activities ceased. Scrutinizing maps and historical documents can reveal that sites used by humans today have been used for much longer than previously thought (e.g. the trail leading to the highest summit of the reserve or those along the western shores of Lake Hertel). The presence of mature *L. terrestris* individuals close to these trails may well be a legacy of a long history of human disturbance and visitation. Without a good characterization of the history of human activities, it would be difficult or impossible to explain the presence of the late-successional earthworms such as *L. terrestris* in sites at 400 m elevation (close to the highest elevation in the reserve) or more than 1,200 m from Lake Hertel. Similarly, sites invaded by two or more species of non-native plants are all proximal to these same historical disturbances. Collectively, these examples in the distribution of non-native earthworms and plants indicate that a long-term perspective is crucial to fully understanding how anthropogenic disturbances influence present-day invasion patterns in this mature forest.

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