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ORIGINAL PAPER

Invasive lianas are drivers of and passengers to altered soil nutrient availability in urban forests

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Abstract Lianas (woody vines) are a leading concern in urban forest management given their ability to reduce the growth rate and survival of trees. Efforts to control invasive lianas are widespread, yet forests are often reinvaded following management. Changes in soil nutrient availability could help explain why some forests are susceptible to reinvasion. Specifically, invasive lianas could be "drivers" of altered nutrient dynamics that persist in the soil and favor their re-establishment, or they could be "passengers" of conditions created by prior site disturbances. We test these alternative models by analyzing soils across gradients of liana cover and forest disturbance in mature hardwood forests in New York City. Overall, total non-native liana cover was linked to elevated soil pH, reduced labile carbon, and altered net potential nitrification—three conditions indicative of increased soil nutrient availability. However, the effects of lianas varied substantially by species. Non-native lianas had a positive, negative, neutral, or non-linear effect on a single soil variable depending on the species. Aggregation of total non-native liana cover can therefore obscure the direction and magnitude of species-level effects. We also found positive relationships between forest disturbance, non-native liana cover, and soil pH, but we found no relationships between disturbance and net nitrification or labile carbon. These results suggest that non-native lianas are passengers to elevated levels of disturbance and soil pH but drivers of altered carbon and nitrogen dynamics. As such, management efforts aimed at reducing soil nutrient availability and removing invasive lianas may be required to limit reinvasion and promote ecosystem recovery.

Keywords Aboveground-belowground interactions · Disturbance · Forest ecology · Nitrogen · Plant-soil feedbacks · Restoration

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Introduction

Urbanization is a dominant pattern of land use that alters ecosystem structure and function in multiple

biomes (Alberti 2005). As urban centers expand to accommodate the growing global population, natural areas will face increasing pressure as a result of human settlement (Seto et al. 2012; Güneralp and Seto 2013). Potential impacts include fragmentation (Luck and Wu 2002), soil disturbance (Pavao-Zuckerman 2008), and invasion by non-native species (Kowarik 2011). These changes can alter ecosystem processes, including carbon (C), water, and nutrient cycling (Alberti 2005; Kaye et al. 2006). In an effort to counter these impacts, cities worldwide are investing in restoration projects that enhance the social and ecological value of natural areas (Pataki et al. 2011; Johnson and Handel 2016). One of the most common and costly restoration measures is invasive species management (Daniels et al. 2016; Pregitzer et al. 2019).

Urban natural areas face frequent and sustained pressures from plant invasions due to high levels of fragmentation, heavy recreational use, altered site conditions, and high propagule pressure (Kowarik 2011; Cadotte et al. 2017). Of the most common invaders, lianas (woody vines) are a leading concern in urban forest management (Green Seattle Partnership 2006; Leicht-Young and Pavlovic 2015; Pregitzer et al. 2018b). The abundance of lianas is increasing worldwide in response to drivers of global change, including elevated temperatures, CO_2 concentrations, and fragmentation (Phillips et al. 2002; Londre and Schnitzer 2006; Schnitzer and Bongers 2011; Laurance et al. 2014). Cities tend to magnify these conditions through their physical structure and emissions (Carreiro and Tripler 2005; George et al. 2007; Lahr et al. 2018), suggesting that urban areas may be particularly suitable for the growth and proliferation of lianas (Brice et al. 2014). Compared to tropical systems, however, temperate lianas remain relatively understudied (Londre and Schnitzer 2006; Ladwig and Meiners 2014; Matthews et al. 2016). Yet human disturbance and warming appear to be facilitating the spread of lianas toward more polar latitudes, thereby increasing their importance in temperate systems (Londre and Schnitzer 2006; Allen et al. 2007; Bradley et al. 2010). Once established, lianas can have substantial and prolonged impacts on the structure, composition, and function of forests (Schnitzer and Bongers 2002; Phillips et al. 2005; Verbeeck and Kearsley 2016). By reducing the growth rate, survival, and regeneration of trees (Ladwig and Meiners 2009, 2010; Ingwell et al. 2010; Matthews et al. 2016), lianas can alter patterns of forest succession (Schnitzer et al. 2000; Tymen et al. 2016) and reduce C storage (van der Heijden et al. 2015).

In addition to altering tree performance and forest structure, lianas also impact belowground processes (Powers 2014; Bray et al. 2017). Woody vines invest in large canopies with high leaf area ratios, and their foliage is often more nutrient rich than leaves from overstory trees (Asner and Martin 2012; Powers 2014). Invasive plants also tend to have higher aboveground productivity and tissue nutrient concentrations than native species (Leishman et al. 2007; Jo et al. 2015a). Non-native liana invasions could therefore alter local C and nitrogen (N) dynamics by shifting the quantity and quality of leaf litter inputs (Hobbie 1992; Bardgett and Wardle 2010; Laughlin 2011; Bray et al. 2017). These changes could persist as legacy effects following the removal of invasive vines for restoration (Ehrenfeld 2003; Lee et al. 2012; Suseela et al. 2016). Elevated soil resource levels may, in turn, give fast-growing, invasive lianas a competitive advantage over native species (Davis et al. 2000), resulting in positive feedbacks that facilitate further invasion (Ehrenfeld 2003; Suding et al. 2004).

Previous work on the ecosystem impacts of invasive plants has focused on their capacity to alter soil nutrient dynamics (Ehrenfeld 2003; Corbin and D'Antonio 2004; Liao et al. 2008, Castro-Díez et al. 2014; Suseela et al. 2016; Bray et al. 2017). Although theories regarding the invasibility of a site often link plant invasions to disturbance (Davis et al. 2000; Moles et al. 2012; Lockwood et al. 2013), altered forest disturbance regimes can also affect soil nutrient availability (Johnson and Curtis 2001; Keiser et al. 2016; Sokol et al. 2017). As such, invasive plants could be "passengers" of altered disturbance regimes or "drivers" of changes in ecological processes (MacDougall and Turkington 2005). Invasive plants could also be "backseat drivers" of ecosystem change; that is, disturbance initially facilitates the invasion, but the introduced species causes further changes to soil processes post-establishment (Bauer 2012). Each of these three models ultimately requires a different management approach (Suding et al. 2004; Didham et al. 2005; Bauer 2012). If invasive plants are passengers of altered disturbance regimes, restoration of prior site conditions is required to limit reinvasion (Didham et al. 2005; Bauer 2012). If invasive plants are drivers of change, removal of the invader is

required to promote the recovery of native-dominated plant communities (Didham et al. 2005; Bauer 2012). If invasive plants are backseat drivers of change, management efforts should prioritize both the restoration of site conditions and invasive species removal to promote ecosystem recovery (Bauer 2012). Understanding the extent to which invasive lianas are passengers, drivers, or backseat drivers of changing ecological conditions is critical for implementing forest management practices that minimize reinvasion.

Here we use observational data to analyze the relationships between native and non-native lianas, disturbance (e.g. canopy gaps), forest structure (e.g. basal area, stem density), and soil nutrient dynamics in temperate urban forests in the northeastern U.S. We demonstrate how observational datasets, which are more readily available to land managers than experimental data, can be used to evaluate the three aforementioned species invasion models. Specifically, we test the following hypotheses (illustrated in Fig. 1): (1) if lianas are passengers to ecosystem change, then liana cover is positively associated with forest disturbance and disturbance also explains the variation in soil processes associated with lianas; (2) if lianas are drivers of ecosystem change, then liana cover is not associated with disturbance levels and disturbance cannot explain the changes in soil processes associated with lianas; or (3) if lianas are backseat drivers of ecosystem change, then disturbance drives variation in liana cover but does not explain changes in soil processes associated with lianas. We tested these three hypotheses using three sets of models: (1) liana cover as a function of forest structure and disturbance, (2) soil processes as a function of forest structure and disturbance, and (3) soil processes as a function of liana cover. Land managers specifically target non-native species for removal, so we also compare the relative effects of native and non-native lianas on soil nutrient availability.

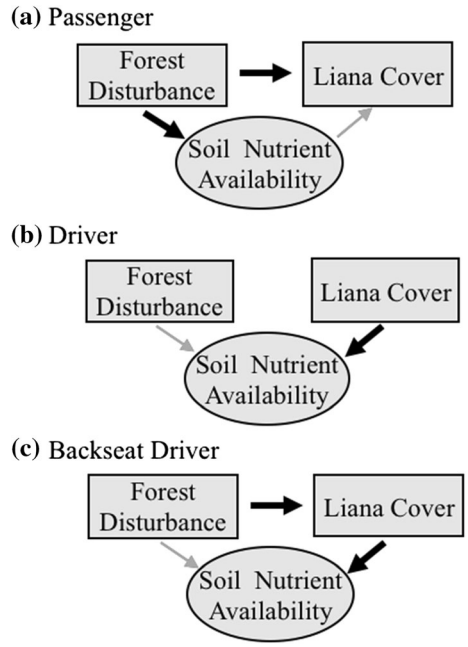

Fig. 1 Conceptual models illustrating three contrasting causative relationships between forest disturbance, liana cover, and soil nutrient availability. Specifically, lianas could be **a** passengers, **b** drivers, or **c** backseat drivers of changing soil nutrient dynamics (MacDougall and Turkington 2005; Bauer 2012). Black arrows depict causative pathways of change, and gray arrows depict relationships that might exist but are immaterial given the primary causative relationships. Predictor and response variables are indicated by rectangles and ovals, respectively. The variables at the origins of the black arrows indicate where management interventions would be required to promote ecosystem recovery in each of the three models

Methods

Study area and site selection

Our work was conducted in New York City's (NYC) Ecological Assessment plots, which were established by the Natural Areas Conservancy in 2013 to provide baseline data to inform forest management objectives (Forgione et al. 2016; Pregitzer et al. 2018a). New York City has a moist, temperate climate with an average winter temperature of 2 °C, an average summer temperature of 24 °C, and a mean annual precipitation of 118 cm (NOAA 2010). Overall, NYC includes 4266 hectares of forests, 2947 of which are actively managed by the Department of Parks and Recreation (Pregitzer et al. 2018a, b). New York City is also a global hotspot of plant invasions (Dawson et al. 2017). Non-native vines are present in canopy trees in over half of NYC's forests, and the most abundant understory species are native and non-native lianas, such as poison ivy (*Toxicodendron radicans* (L.) Kuntze), Virginia creeper (*Parthenocissus quinqefolia* (L.) Planch.), and Japanese honeysuckle (*Lonicera japonica* Thunb; Pregitzer et al. 2018a).

For this study, we used the Ecological Assessment plots classified as mature hardwood forests (n = 414). For detailed methods on site selection for the Ecological Assessment, see Pregitzer et al. (2018a). The majority of hardwood forest plots were underlain by glacial soils, so we excluded 18 plots with soils derived from human transported materials (i.e. topsoil relocation) and/or anthropogenic deposits (i.e. fill; New York City Soil Survey Staff 2005). We also excluded four plots with missing canopy transparency measurements. The final dataset included 392 plots from 23 parks across the five NYC boroughs (Fig. 2). Dominant forest types in these plots included oak-hickory (*Quercus-Carya,* n = 156), oak-tulip poplar (*Quercus-Liriodendron,* n = 138), and oak-beech (*Quercus-Fagus*, n = 51).

We selected a subset of the 392 plots for detailed soil analyses. To identify the subset, we focused only on oak-hickory forests—the most abundant forest type both within NYC and across the eastern U.S. (Oswalt et al. 2014; Pregitzer et al. 2018a). We limited our soil sampling to oak-hickory forests to control for variation in dominant overstory species composition, which can strongly influence C and N mineralization rates (Hobbie 1992; Prescott 2002). We excluded sites located on Staten Island (one of NYC's five boroughs) owing to the heavy influence of white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) browse on understory plant communities.

To select plots that captured a range of native and non-native liana covers, we divided the remaining oak-hickory plots (n = 109) into three liana cover classes using vegetation data collected in the

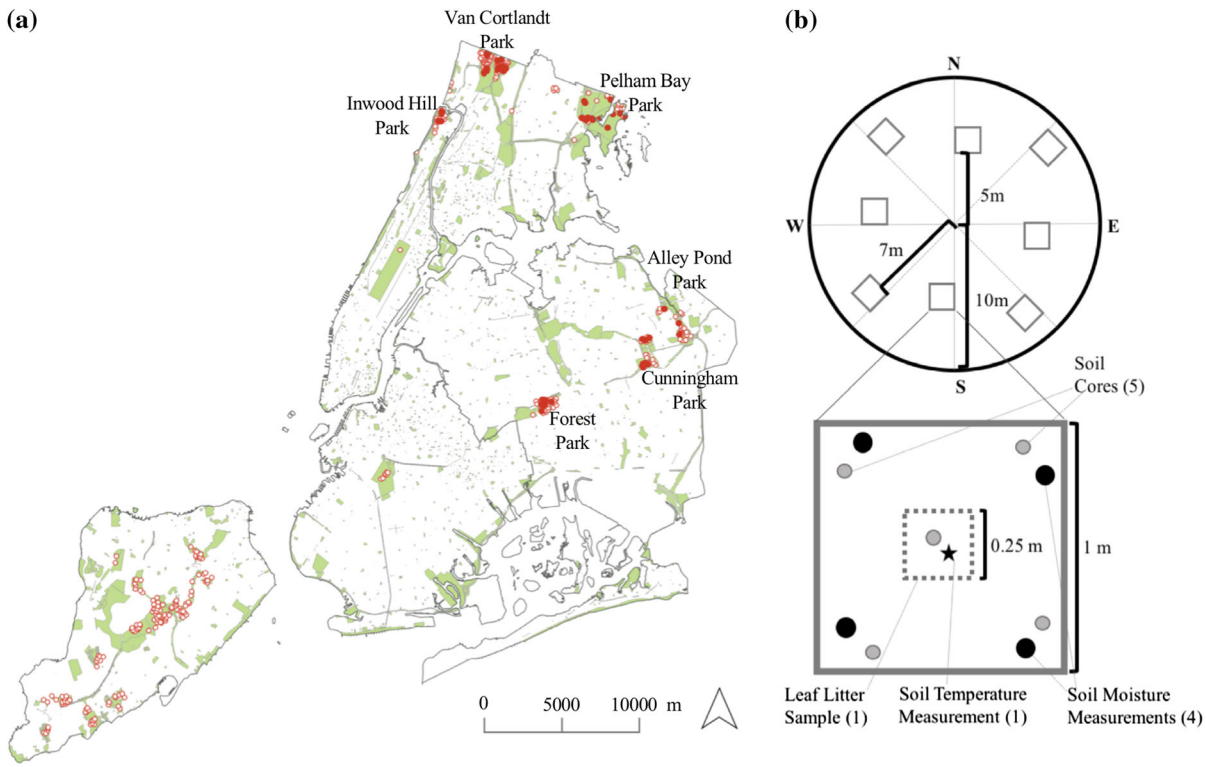

Fig. 2 Map of the plot locations (**a**) and sampling design (**b**). Closed circles show the locations of the subset of oak-hickory forest plots sampled for detailed soil and vegetation analyses in 2017 (n = 54), and open circles show the additional mature hardwood forest plots sampled in 2013–2014 (n = 392). Shaded areas indicate land managed by the New York City Department of Parks and Recreation. Parks containing plots where the 2017 soil sampling occurred are labeled. Each 10 m radius forest plot sampled in 2017 contained eight nested 1 m^2 subplots used to assess understory liana cover. We also collected five soil samples, four volumetric soil moisture measurements, one soil temperature measurement, and one 0.25 m^2 leaf litter patch within each of the eight subplots. Note that the 2013-2014 vegetation assessment included four nested 1 m^2 quadrats used for understory vegetation sampling rather than eight (see Methods)

2013–2014 Ecological Assessment (see next section). We classified "native" species as those listed as native to New York state and "non-native" species as those listed as introduced to New York state (USDA and NRCS 2018). We included species designated as "vine," "vine/subshrub," and "vine/shrub" as lianas, and we excluded any species also designated as "forbs/herbs" (USDA and NRCS 2018). Low liana cover plots had less than 12.5% total liana cover (n = 55), intermediate plots had greater than 12.5% total liana cover but less than 12.5% non-native liana cover (n = 30), and high non-native plots had greater than 12.5% non-native liana cover (n = 24). The 12.5% cutoff enabled us to include at least one plot per liana cover class for six parks in three NYC boroughs: Alley Pond (Queens), Cunningham (Queens), Forest (Queens), Inwood Hill (Manhattan), Pelham Bay (Bronx), and Van Cortlandt (Bronx; Fig. 2, Table S2). We selected 18 plots from each liana cover class, giving us a total of 54 plots in which to sample soils and leaf litter (Fig. 2). Non-native liana covers ranged from 0 to 3.3% ($\bar{x}$ = 0.7%) for the low plots, 0 to 12.0% ($\bar{x}$ = 6.2%) for the intermediate plots, and 12.8 to 65.8% ($\bar{x}$ = 28.4%) for the high plots. Native liana covers ranged from 0 to 10.8% ($\bar{x}$ = 2.8%) in the low plots, 1 to 46.8% ($\bar{x}$ = 18.5%) for the intermediate plots, and 0 to 38.3% ($\bar{x}$ = 17.0%) for the high plots.

To compare the distribution and abundance of liana species in the 54 oak-hickory plots to those in the 392 hardwood forest plots, we calculated the relative abundance and frequency of each liana species in each set of plots. We calculated relative percent cover by dividing the combined cover of each species across all plots by the sum of the covers of all species observed in all plots. We calculated frequency by dividing the number of plots where each species occurred by the number of plots sampled. Given that composition of liana species in the 54 oak-hickory plots measured in 2017 was consistent with the 2013–2014 Ecological Assessment of the 392 mature hardwood forest plots from which we sub-sampled (Table S3), we used the 54 oak-hickory plots to examine the relationships between liana cover, forest disturbance, and soil processes.

Oak-hickory forests typically occur on well-drained ridge tops and south- and west-facing slopes (Edinger et al. 2014). Soils are primarily of glacial origin and include deep, well-drained ablation till (Charlton, Chatfield, and Hollis Series); mesic, fertile basal till of drumlins (Paxton, Montauk, and Woodbridge Series); moderately well-drained glacial outwash (Sutton Series); and poorly drained glaciolacustrine deposits (Tonawanda Series; NRCS Soil Survey Staff 2017; Table S1). Anthropogenic soils derived from locally-excavated upland loams are also found in some of NYC's oak-hickory forests (Greenbelt Series; NRCS Soil Survey Staff 2017; Table S1). Common overstory species include red, black, and white oaks (*Quercus rubra* L., *Q. velutina* Lam., *Q. alba* L., respectively) and shagbark, bitternut, and mockernut hickories (*Carya ovata* (Mill.) K. Koch, *C. cordiformis* (Wangenh.) K. Koch, *C. tomentosa* (Lam.) Nutt., respectively; Edinger et al. 2014).

Liana cover as a function of forest structure and disturbance

We collected data on forest structure, understory vegetation composition and cover, and forest disturbance for the 392 mature hardwood plots from May to October in 2013 and 2014. We identified all living and standing dead trees $\geq$ 2-cm diameter at breast height (DBH, 1.37 m) and recorded DBH of all overstory trees ($\geq$ 10-cm DBH). We estimated the percent cover of understory plant species to the nearest 1% using four 1-m^2 subplots placed 5-m from plot center in each cardinal direction. To estimate canopy transparency, we took four regular canopy photographs per plot at 1.37-m height 5-m from plot center in each cardinal direction and quantified the number of light and dark pixels in each image (Cellprofiler™; Jones et al. 2008). We also visually estimated the percent cover of canopy gaps in each 10-m radius plot. To calculate the percent cover of human disturbance within the plot, we summed the covers of trash, illegal use (e.g. camping, vandalism), infrastructure, recreation (e.g. golf course, evidence of mountain biking), paths, and roads. We calculated the proportion of forest cover surrounding each plot by clipping a land-cover classification map to a 40-m plot buffer in ArcGIS (ESRI, Redlands, California, US). Details on the land-cover map can be found in O'Neil-Dunne et al. (2014). We considered areas classified as upland forest, maritime forest, forested wetland, or other tree canopy as "forests." Non-forest classes included freshwater wetlands, tidal wetlands, upland grasses/scrub, maintained lawns/shrubs, freshwater aquatic vegetation,

saltwater aquatic vegetation, buildings, roads/railroads, other paved surfaces, and bare soil.

Soil processes as a function of forest structure, disturbance, and liana cover

We conducted additional soil and vegetation sampling in the 54 oak-hickory plots in July 2017. We estimated the percent cover of each understory liana species to the nearest 1% in eight 1-m^2 subplots (Fig. 2). Percent liana cover was highly variable both within and between plots. For example, a single plot could contain 100% liana cover in 25% of the plot area, 50% liana cover in 50% of the plot area, and 0% liana cover in the remaining 25% of the plot area. Therefore, to ensure that we collected soil samples across the range of liana densities within each 10-m radius plot, we employed a stratified systematic sampling design. We placed the eight 1-m^2 subplots 5-m from plot center in each cardinal direction and 7-m northeast, southeast, southwest, and northwest from plot center (Fig. 2). We estimated the percent cover of lianas within the eight 1-m^2 subplots using four liana cover bins: < 1%, 1–30%, 31–60%, and > 60% liana cover (Table S2). If this arrangement resulted in only one subplot for one of the liana cover bins, we shifted a single subplot clockwise to ensure that there were at least two subplots per liana bin present.

Within each of the eight 1-m^2 subplots, we also measured volumetric water content (VWC) and collected soil and leaf litter samples (Fig. 2). We measured VWC to a depth of 12 cm in the four corners of each subplot using an HS2 HydroSense Soil Moisture Probe (Campbell Scientific, Logan, UT, USA, Fig. 2). We collected 2-cm diameter, 10-cm deep soil cores from the four corners and center of each subplot and one leaf litter sample from a 0.25-m^2 quadrat in the center of each subplot (Fig. 2). We pooled the soil and leaf litter samples by the four liana cover bins to minimize the influence of fine-scale spatial heterogeneity on our analysis. Each of the 54 plots could therefore contain up to four distinct soil and leaf litter samples (Table S2). In total this generated 94 pooled soil samples and 93 pooled leaf litter samples (one sample had no litter layer; Table S2). We kept field collected soils in coolers and stored them at 4 °C for 5 weeks prior to their analysis.

For the 94 pooled soil samples, we measured a suite of soil properties and processes associated with C and N cycling: pH, gravimetric water content (GWC), water holding capacity (WHC), active microbial biomass, soil organic matter (SOM), C mineralization (labile C), net potential N mineralization, and net potential nitrification. Prior to analysis, we homogenized and then passed the samples through a 2-mm sieve. For pH, we mixed each sample with water in a 1-to-1 volumetric ratio and measured the pH of the supernatant after 10 min using a benchtop meter (VWR sympHony Sb70p; Allen 1989). We determined GWC by weighing, oven drying to constant mass at 105 °C, and re-weighing each sample. We estimated WHC by saturating the soil and allowing it to drain freely for 2-h (Paul et al. 2001). For active microbial biomass (Wardle and Ghani 1995), we used a modified substrate-induced respiration method that measures rates of CO_2 efflux over a 4-h incubation period using an Infra-Red Gas Analyzer (Li-COR model Li-7000; West and Sparling 1986). We estimated SOM by calculating mass loss of soils heated at 375 °C for 18-h in a muffle furnace (Nelson and Sommers 1996). We estimated microbially-available C concentrations using a C mineralization assay that determines potential CO_2 production rates over a 28-day incubation period at 20 °C (Fierer et al. 2005; Bradford et al. 2008). The resulting estimate of "labile C" was calculated as the cumulative CO_2 efflux over the course of the incubation period through integration of five measurement points (1, 4, 11, 21, and 28 days). Finally, to determine potential rates of net N mineralization and net nitrification, we used a 28-day N mineralization assay (Hart et al. 1994; Robertson et al. 1999). For the initial extractions, we added 25 mL 2 M KCl to each soil sample (6-g dry weight equivalent), shook vigorously, refrigerated the soils for 12 h, and filtered the samples. For the incubated samples, we stored 6-g dry weight equivalent of each soil sample at 20 °C and 100% humidity for 28 days with a Parafilm cover to allow air diffusion with minimal moisture loss. We adjusted the soil water content weekly to maintain 65% WHC, which is within the optimal range for microbial activity (Paul et al. 2001; Langenheder and Prosser 2008). After 28 days, we extracted the incubated samples following the same protocol as the initial samples. We analyzed NH_4^+ and NO_3^- concentrations using a flow analyzer (Astoria 2, Astoria-Pacific, Clackamas,

Oregon, USA). Net potential nitrification is the difference in [NO_3^-] between the incubated and initial samples, and net potential N mineralization is the difference between the initial and final sum of [NH_4^+] and [NO_3^-] over the 28-day incubation period.

Statistical analysis

We used linear mixed models (LMMs) to analyze the relationships between liana abundance, forest structure, forest disturbance, and soil processes. Specifically, we ran three sets of models to examine our data in light of the relationships describing lianas as passengers, drivers, or backseat drivers of altered soil nutrient availability: (1) lianas as a function of forest structure/disturbance (n = 392), (2) soil processes as a function of forest structure/disturbance (n = 54), and (3) soil processes as a function of liana abundance (n = 94).

For the first set of models, we used the 392 mature hardwood forest plots sampled in 2013–2014. Response variables included percent cover of all native lianas, all non-native lianas, and the six most abundant liana species. We arcsine square root-transformed all dependent variables to meet assumptions of normal residual distributions and homoscedasticity. We included percent canopy gap, percent human impact, percent canopy transparency, percent forest cover in a 40-m plot buffer, tree stem density (living trees > 2-cm DBH), and overstory basal area as fixed effects. We also included park nested within NYC borough as random effects to account for potential spatial associations between nearby plots.

For the latter two groups of models, we focused on three soil response variables collectively indicative of plant N availability: pH, net potential nitrification, and labile C. Soil pH is a master variable governing biological and chemical processes that affect plant nutrient uptake, with less acidity usually indicative of higher nutrient availability (Brady and Weil 2008). Net potential nitrification is indicative of inorganic N availability (Robertson et al. 1999), and labile C is indicative of the C to N limitation of soil microbes where low labile C suggests that N is not limiting to microbial growth and is therefore more available to plants (Hart et al. 1994; Kaye and Hart 1997; Booth et al. 2005; Keiser et al. 2016). We analyzed the data using hydrogen ion concentration (i.e. the inverse log of pH; [H^+]) instead of pH since it is on a linear rather than logarithmic scale. However, to meet assumptions of normality and homoscedasticity, we natural log-transformed [H^+] and labile C.

For the second set of models describing soil processes as a function of forest structure and disturbance, we included the same fixed and random effects as the first set of models. We used the soil data collected from the 54 oak-hickory plots sampled in 2017 and the forest structure and disturbance data collected from the same plots in 2013–2014. For plots with multiple soil samples (Table S2), we averaged soil measurements by plot since we recorded the disturbance data at the scale of the 10-m radius plots.

For the third set of models describing soil processes as a function of liana cover, we used soil and liana data from the 94 stratified subplots sampled in 2017. Using eight separate models, we tested the effects of all non-native lianas, all native lianas, and the six most abundant liana species on the three soil response variables. For these models, we included plot nested within park as random effects. Due to collinearity (i.e. square root of variance inflation factor (VIF) values > 2) amongst the soil variables measured, which is to be expected for soil process data (Oldfield et al. 2018), we were unable to include all variables measured in the LMMs. Therefore, we chose two variables as covariates known to strongly affect the magnitude of microbially-mediated biogeochemical processes: VWC and microbial biomass (Bradford et al. 2017). The general expectation was that liana cover would increase soil nutrient cycling; however, it was unknown whether these relationships would be linear, asymptotic, unimodal, etc. Therefore, we also tested a quadratic liana cover term in each model and retained it when it improved the model fit ($p < 0.1$).

We tested all independent variables included in the LMMs for collinearity, and the square roots of the VIFs were less than 2 with the exception of the expected correlations between first- and second-order terms in the quadratic models. We tested the models for highly influential observations based on Cook's D but found no grounds for the exclusion of data points. We also tested model robustness by omitting observations with liana cover values of zero and re-running the analysis. The coefficients were not substantially affected by this change, so we retained all observations in the final models. We considered coefficients with $p < 0.05$ to be significant and

coefficients with $p < 0.10$ to be marginally significant. We estimated variance explained by calculating R^2 values for the LMMs using the method described in Nakagawa and Schielzeth (2013). We standardized all predictor variables by subtracting the mean and dividing by one standard deviation, which allowed us to compare the relative effect size of each variable. To examine the influence of changing liana cover on net potential nitrification, $[H^+]$, and labile C, we used the unstandardized coefficients from the LMMs to plot regression lines. Holding microbial biomass and soil moisture constant at their mean values (16.4% and 3.6 μg C g^{-1} h^{-1}, respectively) we varied percent liana cover across its range of observed values to isolate the effect of lianas (Bradford et al. 2017). We fit the models using a Gaussian error distribution and ran all analyses with the 'lme4' package in the statistical freeware R (version 3.4.2; R Core Team 2013; Bates et al. 2015).

Because we observed strong species-specific effects between lianas and soil processes, we ran a post hoc analysis on all the soil and leaf litter variables to characterize patterns between the individual species and soil conditions. Specifically, we were interested in visualizing whether the relationships between lianas and soil processes differentiated by species. Multivariate ordination extracts the main trends of a large dataset in the form of continuous axes to depict broad patterns amongst sites (Borcard et al. 2011). Ordination methods for significance testing do exist (i.e. constrained ordination), but we chose to use a descriptive method (i.e.unconstrained ordination) due to the post hoc nature of the analysis. Unconstrained ordination is used to characterize data structure, but there are no statistical tests to assess the significance of observed patterns (Borcard et al. 2011).

We chose principal component analysis (PCA) as our ordination method due to the high level of collinearity amongst the soil variables in our dataset. PCA reduces the dimensionality of highly correlated variables while still accounting for the majority of variance (Gotelli and Ellison 2004; Borcard et al. 2011; Legendre and Legendre 1998). Prior to running the PCA, we natural log-transformed microbial biomass, labile C, SOM, WHC, GWC, and volumetric soil moisture to achieve normal distributions and linear relationships which improve PCA performance (Legendre and Legendre 1998). We also square root-transformed leaf litter mass and cubic root-transformed $[H^+]$. Continuous supplementary variables not included in the PCA can be plotted using their correlations with the axes of PCA biplots (Graffelman and Aluja-Benet 2003). Therefore, we calculated the correlation coefficients between the scores of the first two principal components and the six most abundant liana species (Table S6). Analyses and visualization were performed using the "ggplot2" and "ggfortify" packages in R (Wickham 2016; R Core Team 2013; Tang et al. 2016).

Results

Liana cover as a function of forest structure and disturbance

We identified six native and eight non-native lianas in the 2017 survey of the 54 oak-hickory plots giving us a total of 14 species (Table S3). The two most abundant species—*T. radicans* (poison ivy) and *P. quinqefolia* (Virginia creeper)—were both native (Table S3). The four most abundant non-native species—*Celastrus orbiculatus* Thunb. (oriental bittersweet), *Rosa multiflora* Thunb. (multiflora rose), *L. japonica* Thunb. (Japanese honeysuckle), and *Ampelopsis brevipedunculata* (Maxim.) Trautv (porcelainberry)—were all classified as invasive in New York state (BBG and TNC 2013).

Disturbance and forest structure explained approximately 12% of the variation in non-native liana cover (Table 1). The coefficients for percent canopy gap, percent forest cover in the plot buffer, percent human impact, and tree stem density all had significant effects on total non-native liana cover (Table 1). Percent canopy gap had the strongest effect, and the relationship was positive ($p < 0.001$; Table 1). Plots that overlapped with canopy gaps had, on average, over twice the non-native liana cover (8.6 ± 0.9% $\bar{x}$ ± SE, n = 231) as plots with no canopy gaps (3.7 ± 0.5% $\bar{x}$ ± SE, n = 161). Plots with greater than 20% canopy gap coverage had over five times the percent cover of non-native lianas (18.7 ± 3.1% $\bar{x}$ ± SE, n = 40) relative to plots with no canopy gaps. Two of the four individual non-native species—*C. orbiculatus* and *A. brevipedunculata*—were also positively associated with canopy gap coverage ($p < 0.01$ for both). Total non-native liana cover, *L. japonica* cover, and *A. brevipedunculata* cover were also negatively related

Table 1 Standardized coefficients (mean ± SE) for the linear mixed models used to evaluate the effects of forest disturbance and structure on both liana cover and soil nutrient availability. Note that the first four columns are repeated in the bottom half of the table to clarify that all six forest structure and disturbance variables are included together in the each of the models

Model group	Response variable	*n*	Fixed R^2 (Full)	Predictor variables			
				Intercept	Canopy gap (%)	Human impact (%)	Canopy transparency (%)
Lianas ~ forest disturbance	All non-native Lianas	392	12 (25)	**0.16 ± 0.019**	**0.045 ± 0.011**	**− 0.023 ± 0.0099**	0.0084 ± 0.011
	C. orbiculatus		6.5 (16)	**0.055 ± 0.011**	**0.021 ± 0.0070**	− 0.0069 ± 0.0062	0.0097 ± 0.0070
	R. multiflora		2.4 (31)	**0.063 ± 0.017**	0.011 ± 0.0074	− 0.0048 ± 0.0066	0.00060 ± 0.0073
	L. japonica		11 (16)	**0.059 ± 0.0085**	0.011 ± 0.0066	**− 0.015 ± 0.0056**	0.0070 ± 0.0066
	A. brevipedunculata		7.6 (11)	**0.016 ± 0.0046**	**0.010 ± 0.0039**	− 0.0030 ± 0.0034	− 0.00051 ± 0.0039
	All Native Lianas		3.7 (20)	**0.23 ± 0.019**	0.016 ± 0.010	− 0.0052 ± 0.0091	0.0061 ± 0.010
	T. radicans		4.5 (25)	**0.12 ± 0.016**	0.0068 ± 0.0079	− 0.011 ± 0.0070	− 0.0075 ± 0.0079
	P. quinquefolia		3.1 (13)	**0.087 ± 0.011**	0.00092 ± 0.0070	− 0.0031 ± 0.0061	0.0030 ± 0.0070
Soils ~ forest disturbance	Net Potential Nitrification	54	16 (26)	**0.88 ± 0.089**	− 0.074 ± 0.064	− 0.0043 ± 0.063	− 0.0031 ± 0.067
	H^+ Concentration*		25 (48)	**− 12.4 ± 0.29**	**− 0.35 ± 0.14**	− 0.18 ± 0.14	− 0.12 ± 0.15
	Labile C*		4.6 (24)	**6.36 ± 0.072**	− 0.059 ± 0.042	0.0054 ± 0.042	0.025 ± 0.045

Model group	Response variable	*n*	Fixed R^2 (Full)	Predictor variables		
				Forest cover in buffer (%)	Stem density (Trees ha^{-1})	Basal area (m^2 ha^{-1})
Lianas ~ forest disturbance	All non-native Lianas	392	12 (25)	**− 0.030 ± 0.010**	**− 0.028 ± 0.010**	− 0.004 ± 0.0094
	C. orbiculatus		6.5 (16)	− 0.0011 ± 0.0062	− 0.0068 ± 0.0063	− 0.00073 ± 0.0059
	R. multiflora		2.4 (31)	− 0.0075 ± 0.0065	**− 0.014 ± 0.0065**	− 0.0035 ± 0.0062
	L. japonica		11 (16)	**− 0.033 ± 0.0059**	− 0.0054 ± 0.0059	− 0.00063 ± 0.0056
	A. brevipedunculata		7.6 (11)	**− 0.0082 ± 0.0035**	**− 0.0085 ± 0.0035**	**− 0.0069 ± 0.0034**
	All Native Lianas		3.7 (20)	− 0.012 ± 0.0091	**− 0.020 ± 0.0091**	**0.017 ± 0.0086**
	T. radicans		4.5 (25)	**− 0.019 ± 0.0070**	**− 0.018 ± 0.0070**	**0.017 ± 0.0066**
	P. quinquefolia		3.1 (13)	− 0.00058 ± 0.0062	*− 0.011 ± 0.0062*	**0.018 ± 0.0059**
Soils ~ forest disturbance	Net Potential Nitrification	54	16 (26)	**0.20 ± 0.070**	0.030 ± 0.068	0.019 ± 0.063
	H^+ Concentration*		25 (48)	**0.50 ± 0.16**	0.20 ± 0.15	− 0.12 ± 0.14
	Labile C*		4.6 (24)	0.018 ± 0.047	− 0.014 ± 0.045	0.0010 ± 0.042

Significant ($p < 0.05$) and marginally significant ($p < 0.1$) coefficients are shown in bold and italic fonts, respectively

*Response variable was natural log-transformed

to the percent forest cover in the 40-m plot buffer ($p < 0.01$, $p < 0.001$, $p < 0.05$; Table 1). Plots with less than 85% forest cover in the buffer had about twice the non-native liana cover (10.9 ± 0.8% $\bar{x}$ ± SE, n = 48) as plots surrounded by 100% forest cover (5.7 ± 0.7% $\bar{x}$ ± SE, n = 217). Total non-native liana cover and *L. japonica* were also negatively related to percent human impact within the plot ($p < 0.05$ and $p < 0.01$, respectively; Table 1). Non-native lianas were generally associated with lower levels of forest structure. All non-native lianas, *R. multiflora*, and *A. brevipedunculata* were negatively related to tree stem density ($p < 0.01$, $p < 0.05$, and $p < 0.05$, respectively), and *A. brevipedunculata* was also negatively related to basal area ($p < 0.05$).

Native liana cover was only associated with the forest structure parameters. Tree stem density had a negative effect on total native liana cover ($p < 0.05$) and overstory basal area had a positive effect ($p < 0.05$), but the overall variance explained by these variables was low (R^2 = 3.7%; Table 1). The individual native species had similar relationships with forest structure. *Toxicodendron radicans* and *P. quinquefolia* were positively associated with basal area ($p < 0.05$ and $p < 0.01$, respectively; Table 1), and *T. radicans* was negatively associated with tree stem density ($p < 0.01$). *Toxicodendron radicans* was also negatively associated with the proportion of forest cover in the plot buffer ($p < 0.01$; Table 1).

Soil processes as a function of forest structure and disturbance

The effects of forest structure and disturbance on pH, net potential nitrification, and labile C in the 54 plots sampled in 2017 were variable (Table 1). Fixed effects in these models explained 25% of the variation in pH, 16% of the variation in net potential nitrification, and only 4.6% of the variation in labile C (Table 1). Elevated soil pH was most closely linked to forest disturbance. On average, the 54 oak-hickory plots were acidic (5.21 + 0.07 $\bar{x}$ pH + SE) but ranged by three orders of magnitude (min pH = 4.73, max pH = 7.24). pH had a strong negative association with the percent forest cover in the plot buffer ($p < 0.01$) and a positive association with the percent canopy gap within the plot ($p < 0.05$; reported as $[H^+]$ in Table 1). Soils were about 60% more acidic in plots without canopy gaps (5.08 + 0.08 $\bar{x}$ pH + SE, n = 17) than in plots with canopy gaps (5.29 + 0.07 $\bar{x}$ pH + SE, n = 37). Soils were also about twice as acidic in plots with 100% forest cover in the plot buffer (5.15 + 0.06 $\bar{x}$ pH + SE, n = 32) than in plots with less than 85% surrounding forest cover (5.50 + 0.15 $\bar{x}$ pH +55 SE, n = 10).

The net potential nitrification rates in our study area ranged from net immobilization (− 0.42 μg N g soil^{-1} days^{-1}) to net nitrification (1.86 μg N g soil^{-1} - days^{-1}) with an average of 0.84 ± 0.05 μg N g soil^{-1} days^{-1}. We found a positive relationship between net potential nitrification and the proportion of forest cover in the plot buffer ($p < 0.01$; Table 1). Plots surrounded by 100% forest cover had net potential nitrification rates that were about 50% higher (0.94 ± 0.06 μg N g soil^{-1} days^{-1} $\bar{x}$ ± SE, n = 32) than plots with less than 85% forest cover in the plot buffer (0.63 ± 0.13 μg N g soil^{-1} days^{-1} $\bar{x}$ ± SE, n = 10).

The average C mineralization rate in our study area was 617.0 ± 24.7 μg C g soil^{-1} days^{-1} and ranged from 320.9 to 1663.1 μg C g soil^{-1} days^{-1}. We found no significant relationships between labile C and the terms included in the forest structure/disturbance model (Table 1).

Soil processes as a function of liana cover

Overall, the LMMs that included liana cover explained over 30% of the variation in pH and net potential nitrification and over 60% of the variation in labile C (Table 2). Notably, total non-native liana cover had either a significant or marginally significant effect on all three soil processes studied (Table 2). In contrast, we found no relationships between native liana cover and soil processes regardless of the species tested (Table 2).

The effects of non-native lianas were strongly species-specific (Table 2, Fig. 3). In some cases, the individual species had similar effects on a particular soil process, which heightened the aggregated effect of total non-native liana cover (e.g. net potential nitrification; Table 2, Fig. 3). In other instances, the effects of non-native lianas differed by species, thereby reducing the combined effect of all non-native lianas (e.g. pH and labile C; Table 2, Fig. 3).

We found a strong positive association between total non-native liana cover and net potential nitrification, and the relationship was unimodal ($p < 0.05$;

Table 2 Standardized coefficients (mean ± SE) for the linear mixed models used to evaluate the effect of liana cover on three soil response variables: net potential nitrification, H^+ concentration, and labile C

Variable	Liana cover type							
	All non-native lianas	Non-native species				All native lianas	Native species	
		C. orbiculatus	*R. multiflora*	*L. japonica*	*A. brevipedunculata*		*T. radicans*	*P. quinquefolia*
Net nitrification								
Intercept	**0.92 ± 0.059**	**0.84 ± 0.044**	**0.84 ± 0.044**	**0.84 ± 0.044**	**0.84 ± 0.044**	**0.84 ± 0.043**	**0.84 ± 0.044**	**0.84 ± 0.043**
Liana cover	**0.21 ± 0.082**	0.060 ± 0.044	0.029 ± 0.044	0.026 ± 0.045	− 0.0044 ± 0.044	0.058 ± 0.044	0.018 ± 0.044	0.050 ± 0.050
(Liana cover)^2	*− 0.076 ± 0.039*	–	–	–	–	–	–	–
Soil moisture	**− 0.27 ± 0.046**	**− 0.28 ± 0.046**	**− 0.30 ± 0.046**	**− 0.29 ± 0.046**	**− 0.29 ± 0.046**	**− 0.30 ± 0.045**	**− 0.29 ± 0.046**	**− 0.30 ± 0.046**
Microbial biomass	0.041 ± 0.045	0.053 ± 0.046	0.048 ± 0.046	0.040 ± 0.046	0.046 ± 0.046	0.036 ± 0.046	0.042 ± 0.046	0.042 ± 0.045
Fixed R^2 (full)	35 (40)	32 (33)	31 (31)	31 (31)	31 (31)	32 (32)	31 (31)	32 (32)
*H^+ Concentration**								
Intercept	**− 12.5 ± 0.14**	**− 12.6 ± 0.12**	**− 12.6 ± 0.12**	**− 12.8 ± 0.12**	**− 12.6 ± 0.11**	**− 12.6 ± 0.12**	**− 12.6 ± 0.12**	**− 12.6 ± 0.12**
Liana cover	*− 0.19 ± 0.11*	0.027 ± 0.11	0.079 ± 0.086	**− 0.75 ± 0.29**	**− 0.30 ± 0.090**	0.030 ± 0.11	− 0.050 ± 0.11	− 0.018 ± 0.11
(Liana cover)^2	–	–	–	**0.12 ± 0.060**	–	–	–	–
Moisture	**− 0.48 ± 0.12**	**− 0.48 ± 0.12**	**− 0.46 ± 0.12**	**− 0.49 ± 0.11**	**− 0.43 ± 0.11**	**− 0.49 ± 0.12**	**− 0.49 ± 0.12**	**− 0.49 ± 0.12**
Microbial biomass	**− 0.52 ± 0.11**	**− 0.51 ± 0.11**	**− 0.40 ± 0.088**	**− 0.47 ± 0.11**	**− 0.37 ± 0.090**	**− 0.52 ± 0.11**	**− 0.52 ± 0.12**	**− 0.51 ± 0.11**
Fixed R^2 (full)	39 (47)	37 (48)	38 (48)	42 (47)	47 (56)	37 (47)	37 (48)	37 (48)
*Labile C**								
Intercept	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**	**6.4 ± 0.022**
Liana cover	*− 0.040 ± 0.021*	− 0.033 ± 0.022	**− 0.049 ± 0.022**	0.025 ± 0.022	**− 0.14 ± 0.07**	0.015 ± 0.022	− 0.0023 ± 0.022	0.029 ± 0.022
(Liana cover)^2	–	–	–	–	*0.020 ± 0.010*	–	–	–
Soil moisture	**− 0.15 ± 0.023**	**− 0.15 ± 0.023**	**− 0.14 ± 0.023**	**− 0.14 ± 0.023**	**− 0.15 ± 0.023**	**− 0.15 ± 0.023**	**− 0.15 ± 0.023**	**− 0.15 ± 0.024**
Microbial biomass	**0.26 ± 0.022**	**0.26 ± 0.023**	**0.26 ± 0.022**	**0.26 ± 0.023**	**0.27 ± 0.023**	**0.26 ± 0.023**	**0.26 ± 0.023**	**0.26 ± 0.023**
Fixed R^2 (full)	62 (64)	62 (64)	63 (66)	61 (64)	62 (65)	61 (64)	61 (63)	61 (64)

Significant ($p < 0.05$) and marginally significant ($p < 0.1$) coefficients are shown in bold and italic fonts, respectively

*Response variable was natural log-transformed

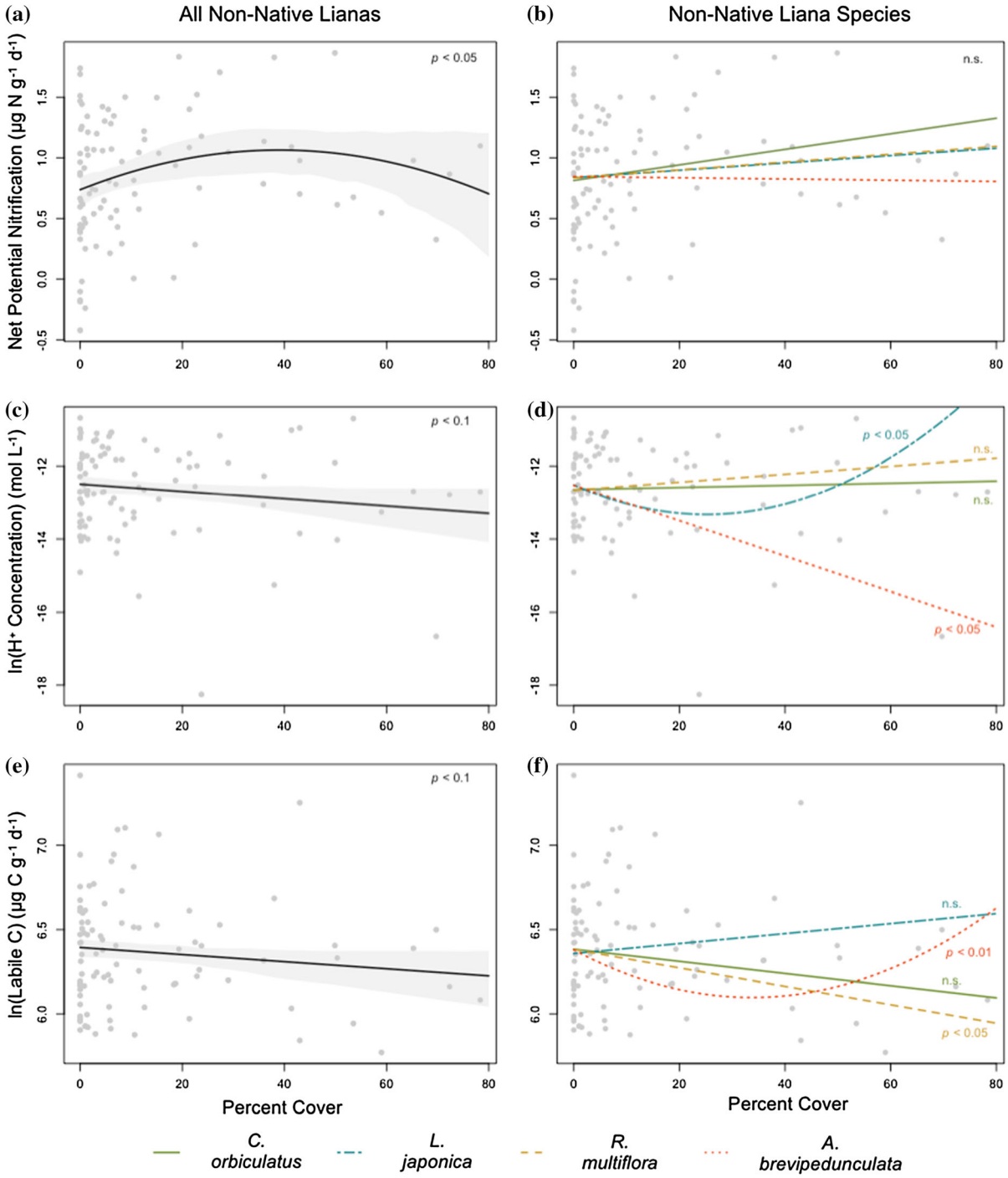

Table 2, Fig. 3). VWC also had a strong negative relationship with net nitrification ($p < 0.0001$; Table 2). Notably, the standardized coefficients for total non-native liana cover and soil moisture were of comparable magnitude, and they were both significantly larger than that of microbial biomass (Table 2). The effect size of non-native liana cover was therefore equal to or larger than two biotic and abiotic factors

◀**Fig. 3** The modeled effects of changing liana cover on net potential nitrification (**a**, **b**), hydrogen ion concentration (i.e. pH, **c**, **d**), and labile C (**e**, **f**). The regression lines are not trendlines but instead depict the modeled relationships between liana cover and the three soil response variables using the unstandardized coefficients from the LMMs (Table S4). Holding all other factors (i.e. microbial biomass and soil moisture) constant at their mean values, we varied percent liana cover across its range of observed values. Note that the scatter in the underlying data points is an outcome of the fact that net potential nitrification, hydrogen ion concentration, and labile C are controlled by multiple variables (Table 2, S4). The regression line then holds these other variables constant (see Methods) to isolate the effect of liana cover. Panels on the left (**a**, **c**, **e**) illustrate relationships for total non-native liana cover while panels on the right (**b**, **d**, **f**) illustrate relationships for the four most abundant non-native liana species observed. For net potential nitrification, the four individual species have similar effects. Thus, their combined effect is significant even though the effects of the individual species are not. In contrast, the four non-native liana species had markedly different effects on labile C and hydrogen ion concentration, so their combined effect is less significant than that of the individual species. Patterns between total non-native liana cover and soil processes can therefore fail to capture species-level effects

known to influence nitrification rates. The four individual non-native lianas all had neutral to positive effects with *C. orbiculatus* having the largest coefficient, followed by *R. multiflora*, *L. japonica*, and *A. brevipedunculata*. However, none of these relationships were significant (Table 2, Fig. 3). Because the non-native liana species all had similar effects on net potential nitrification, the combined effect of total non-native liana cover was significant (Table 2, Fig. 3).

In contrast, individual non-native species had stronger effects on soil pH than total non-native liana cover. The coefficients of two of the four non-native species were significant, and they each had different effects (Table 2). We found a strong positive relationship between *A. brevipedunculata* and soil pH ($p < 0.05$) and a strong non-linear relationship between *L. japonica* and pH ($p < 0.05$; reported as $[H^+]$ in Table 2). The relationship between *L. japonica* and pH was initially positive but strongly negative at intermediate to high *L. japonica* levels (plotted as $[H^+]$ in Fig. 3). When aggregated, however, the relationship between total non-native liana cover and pH was positive and marginally significant ($p < 0.1$; Table 2, Fig. 3). In addition to the effects of non-native lianas, soil moisture and microbial biomass also both had strong positive associations with pH ($p < 0.05$; reported as $[H^+]$ in Table 2). The effect size of *L. japonica* cover was significantly larger than that of both microbial biomass and soil moisture. For *A. brevipedunculata*, the effect sizes of liana cover, microbial biomass, and soil moisture were all comparable.

For labile C, the species-level effects were also stronger than the combined effect of all non-native lianas. We found significant coefficients for two of the four non-native species but only a marginally significant relationship between total non-native liana cover and labile C ($p < 0.1$; Table 2, Fig. 3). Once again, the individual species had notably different effects (Table 2, Fig. 3). *Rosa multiflora* had a significant negative relationship with labile C, and *A. brevipedunculata* had a significant non-linear relationship with labile C ($p < 0.05$ and < 0.01, respectively; Table 2, Fig. 3). The relationship between *A. brevipedunculata* and labile C was initially negative but strongly positive at intermediate to high levels of *A. brevipedunculata* cover (Fig. 3). As expected, microbial biomass had a strong positive effect on labile C whereas soil moisture had a negative effect (Table 2). In the labile C models, microbial biomass had the largest coefficient followed by soil moisture. However, for the *A. brevipedunculata* model, the effects of liana cover and soil moisture were comparable (Table 2).

We supplemented our analysis with a PCA to visualize the species-specific relationships that emerged from the LMMs (Fig. 3). Given the post hoc nature of this analysis, we used the PCA to characterize broad patterns between individual liana species and soil processes rather than for testing a priori hypotheses. The first principal component (PC1) of all soil and leaf litter variables accounted for 36% of the variance and generally corresponded with variables related to C availability (Table S5). Positive loadings of PC1 included VWC and negative loadings included SOM, labile C, WHC, and leaf litter mass (Table S5). The second principal component (PC2) accounted for an additional 29% of the variance (Table S5). Positive loadings of PC2 corresponded with microbial biomass and GWC and negative loadings corresponded with soil acidity (reported as $[H^+]$ in Table S5). Together, PC1 and PC2 accounted for 65% of the variance (Table S5).

We observed species-specific relationships in the PCA biplots consistent with the statistical models described above. The two native species were associated with similar soil processes. *Parthenocissus quinquefolia* and *T. radicans* both had positive associations with PC2 (r = 0.19 and 0.13, respectively) and slight negative associations with PC1 (r = −0.009 and − 0.07, respectively; Table S6). Overall these results indicate that native lianas are associated with higher labile C, microbial biomass, and GWC (Fig. 4, Table S5). In contrast, the relationships between non-native lianas and soil conditions varied substantially by species. For instance, *R. multiflora* and *L. japonica* were most highly correlated with PC1 but in opposite directions (r = 0.17 and − 0.13, respectively; Table S6). Additionally, *C. orbiculatus* and *R. multiflora* were negatively associated with PC2 (r = −0.25 and − 0.10, respectively) whereas *L. japonica* and *A brevipedunculata* were positively associated with PC2 (r = 0.16 and 0.12 respectively; Table S6). The relationships between the individual non-native species and soil processes observed in the PCA biplots are consistent with the LMMs. For instance, *C. orbiculatus* and *R. multiflora* were associated with low labile C, high net nitrification rates, and low pH. In contrast, *L. japonica* was associated with high labile C and *A. brevipedunculata* was associated with high pH values (Fig. 4).

Discussion

Our study provides evidence that non-native lianas are passengers to elevated levels of forest disturbance and soil pH but drivers of altered C and N dynamics. Together, these results indicate that non-native lianas are backseat drivers of changing soil nutrient availability (Fig. 1c). Lianas are typically considered disturbance-adapted plants (Schnitzer and Carson 2001; Pavlovic and Leicht-Young 2011; Schnitzer and Bongers 2011), and we did find a positive relationship between non-native liana cover and forest disturbance. Yet disturbance did not explain all changes in soil processes associated with high non-native liana cover. Specifically, we found a positive relationship between soil pH and forest disturbance but no relationship between disturbance and labile C or net potential nitrification. Prior site disturbance is therefore presumably responsible for reducing soil acidity and promoting the growth of non-native lianas (Fig. 1a). Once established, however, our results suggest that non-native lianas directly alter labile C and net potential nitrification rates (Fig. 1b). Management efforts that exclusively target aboveground vegetation may therefore be insufficient for the restoration of belowground properties, including soil pH (Suding et al. 2004; Didham et al. 2005; Bauer 2012). Moreover, by altering C and N dynamics, invasive lianas could create soil legacies that persist following their removal (Ehrenfeld 2003; Suseela et al. 2016). These changes in soil nutrient availability—driven by both disturbance and non-native lianas—could make forests susceptible to reinvasion following management (Lee et al. 2012). Restoration strategies that address both prior site disturbances and feedbacks between invasive plants and soil nutrient cycling are therefore required to limit reinvasion in urban forests subjected to high levels of human impact (Suding et al. 2004; Pavao-Zuckerman 2008).

Disturbance is often cited as a key driver of species invasions (Moles et al. 2012; Lockwood et al. 2013). Yet it remains unclear whether urbanization and anthropogenic disturbance increase the invasibility of a site directly through reduced biotic competition (Elton 1958) and elevated abiotic resource availability (Davis et al. 2000) or indirectly by increasing human-mediated dispersal of non-native propagules (Colautti et al. 2006). Different disturbance factors can also be drivers of different phases of the invasion process (Lockwood et al. 2013). For instance, many invasive liana species, including porcelainberry (*A. brevipedunculata*), oriental bittersweet (*C. orbiculatus*), and Japanese honeysuckle (*L. japonica*), are shade-tolerant and employ a "sit-and-wait" strategy whereby they persist as seedlings in shaded forest understories and grow rapidly in response to canopy openings (Greenberg et al. 2001; Martin et al. 2009; Pavlovic and Leicht-Young 2011; Ladwig and Meiners 2014). In these instances, proximity to forest edges likely promotes non-native liana establishment by exposing intact forests to increased propagule pressure (Von Holle and Simberloff 2005; Colautti et al. 2006). Canopy gaps, on the other hand, likely promote the growth and spread of invasive lianas by increasing resource availability (Davis et al. 2000). Linking these different factors of forest disturbance to distinct phases of the invasion process suggests a need for an alternate strategy of invasive liana management.

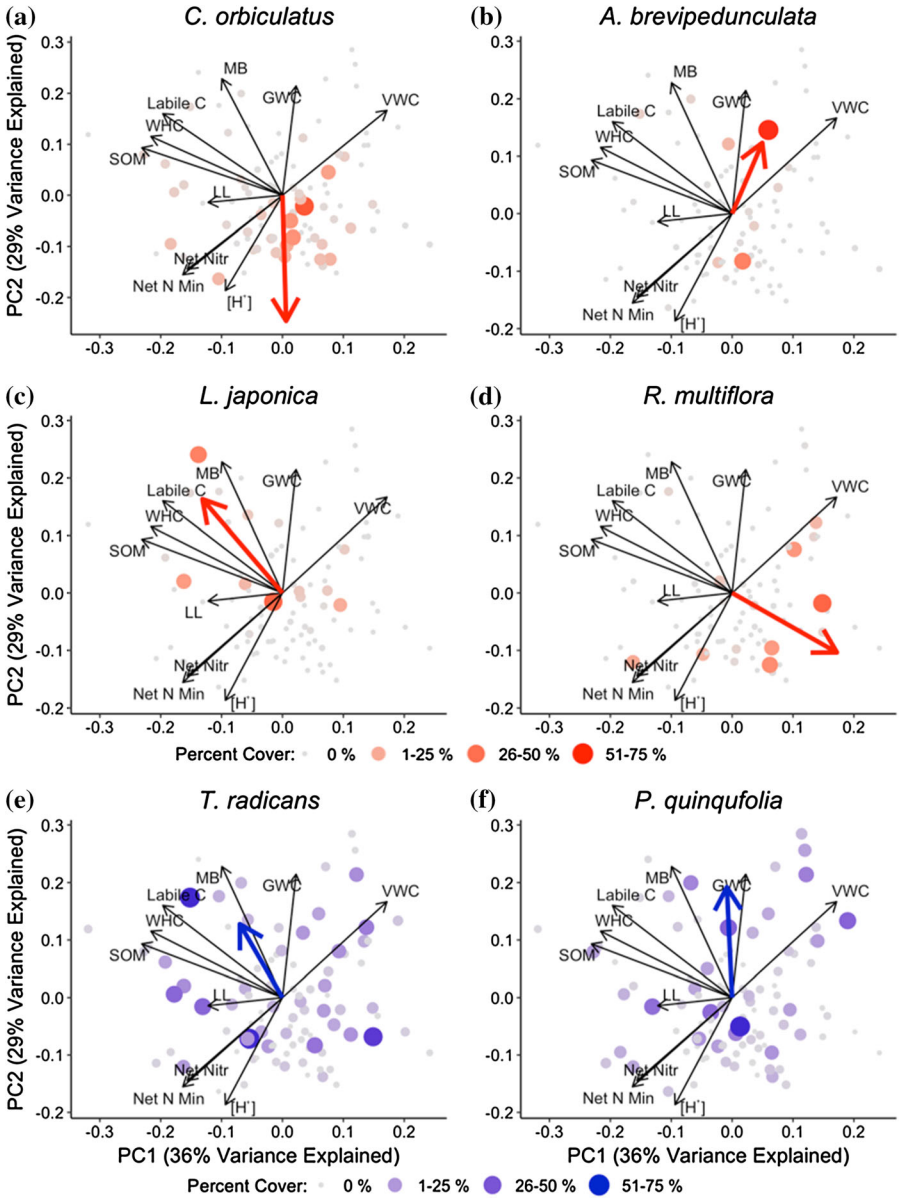

Fig. 4 The four most abundant non-native (**a**–**d**) and two most abundant native (**e**, **f**) percent liana covers overlain on biplots of the first two principal components of ten soil and leaf litter variables (n = 94): microbial biomass (MB), gravimetric water content (GWC), volumetric water content (VWC), hydrogen ion concentration ([H^+]), net potential nitrogen mineralization (Net N Min), net potential nitrification (Net Nitr), leaf litter mass (LL), soil organic matter (SOM), water holding capacity (WHC), and carbon mineralization (Labile C). Percent cover is plotted as a continuous variable with larger values being associated with larger, darker points. Thick arrows depict the correlation coefficients between the percent cover of each liana species and the scores of the first two principal components, with the direction showing the soil variables that higher cover of that species was most strongly associated with. The correlation coefficients indicate that the four non-native species—*Celastrus orbiculatus* (**a**), *Ampelopsis brevipedunculata* (**b**), *Lonicera japonica* (**c**), and *Rosa multiflora* (**d**)—are each associated with distinct soil processes/properties

Highly invaded forests appear to be in greatest need of restoration. However, because the cost and challenge of invasive species removal increases exponentially with the severity of an invasion (Lockwood et al. 2013; Simberloff et al. 2013), increased monitoring and management of intact or recently disturbed forests

with low invasive liana covers could help reduce the cost of their control (Pregitzer et al. 2018b, 2019).

Although invasive species management can drastically shift the structure and composition of urban forests relative to unrestored sites (Johnson and Handel 2016), it may be insufficient for the restoration of ecosystem processes (Suding et al. 2004; Didham et al. 2005; Bauer 2012). For instance, we found that disturbance, rather than liana invasions, likely increases soil pH levels in urban forests. Therefore, removal of target invasive plants is unlikely to raise soil acidity to pre-disturbance levels. Positive associations between urbanization and soil pH are common. Work conducted in the New York metropolitan region documented higher soil pH levels both in urban forests relative to their rural counterparts (Pouyat et al. 2007) and along a gradient of increasing soil disturbance within urban natural areas (Pregitzer et al. 2016). Worldwide, soil pH levels of mesic temperate forests range from 3.0 to 5.0 in water (Osman 2013), and only 19% of our samples (n = 18) fell within this interval. Potential mechanisms driving the positive relationship between urbanization and soil pH include the nearby application of road salts and calcium-enriched water for irrigation as well as weathering of concrete and other anthropogenic materials in landscaped and impervious areas adjacent to forests (Craul 1985; Jim 1998). There is also mounting evidence linking increases in soil pH to plant invasions in temperate deciduous forests (Ehrenfeld et al. 2001; Kourtev et al. 2003; Leicht-Young et al. 2009; Huebner et al. 2014). However, it is unknown whether disturbance per se promotes invasions or whether the process is mediated through concurrent ecological changes, such as heightened pH levels. Additional management efforts aimed at lowering soil pH (e.g. application of elemental sulfur) may therefore be required to restore soil acidity and limit reinvasion (Oldfield et al. 2014; Pregitzer et al. 2016). Land managers could also shift planting palettes to include species more competitive in alkaline soils, such as American basswood (*Tilia Americana* L.) and tulip poplar (*Liriodendron tulipifera* L., Bassuk et al. 2003).

Contrary to previous work (Johnson and Curtis 2001; Keiser et al. 2016; Sokol et al. 2017), we found no relationship between disturbance and net potential nitrification or labile C. Therefore, our results suggest that non-native lianas are drivers of altered C and N availability in urban forests (Fig. 1b). Net potential nitrification rates are typically elevated in urban systems relative to non-urban forests due to anthropogenic N inputs (Pavao-Zuckerman 2008; Reisinger et al. 2016). Indeed, the net nitrification rates we measured were 3–8 times higher than those measured in similar but non-urban forests in the Catskills region outside of NYC (Burns and Murdoch 2005). Therefore, although our study found no relationship between forest disturbance and net nitrification, the urban environment as a whole may still be associated with elevated soil N availability (Kaye et al. 2006; Pavao-Zuckerman 2008; Reisinger et al. 2016), which could potentially increase the susceptibility of urban forests to future invasions.

We also found a positive relationship between non-native liana cover and soil nutrient availability (i.e. elevated pH levels, reduced labile C, and increased net potential nitrification rates) that is consistent with previous work and theory (Hobbie et al. 1992; Davis et al. 2000; Ehrenfeld 2003). Past research has found that plant invaders have the capacity to alter soil C and N cycling and transformation rates, thereby increasing long-term N availability and depleting labile C pools (Liao et al. 2008; Strickland et al. 2010; Kramer et al. 2012; Craig and Fraterrigo 2017). Moreover, a comparative study analyzing leaf decomposition rates for deciduous woody plants in temperate systems found that mass loss of liana litter was up to 75% higher than that of self-supporting species (Cornelissen 1996). By enhancing the quantity and quality of leaf litter inputs, non-native lianas may therefore be increasing C and N cycling rates, which could have long-term impacts on soil fertility. Interestingly, we also found a non-linear relationship between non-native lianas and net potential nitrification. This finding could be explained by the high N acquisition rates and N-use efficiencies of invasive plants, which may result in the sequestration of N in plant biomass in highly invaded sites (Funk and Vitousek 2007; Craig and Fraterrigo 2017). Overall, however, our results suggest that management efforts aimed at reducing soil nutrient availability may be required to create conditions favorable for the establishment of native plants in historically N-limited systems (Perry et al. 2010). For instance, the application of high C:N organic material, such as wood chips, could increase soil acidity while also immobilizing inorganic N.

The effects of non-native lianas on soil nutrient availability also varied substantially by species. These

divergent impacts emphasize the potential importance of studying both the combined and individual effects of co-occurring invaders since the removal of a single species could heighten or dampen the overall community impact (Kuebbing et al. 2013). We also observed that the relationships between total non-native liana cover and soil pH and labile C were relatively weak compared to the species-level effects. Thus, our results show that aggregation of total non-native liana cover can obscure species-specific relationships. This issue, known as the "ecological inference fallacy," occurs when individual-level effects are deduced from grouped data (Robinson 1950; Bradford et al. 2017). Research on invasive plants and their effects on ecological processes have often yielded idiosyncratic results, suggesting that generalizations about the impacts of plants on nutrient cycling based on species' origin may not be particularly useful (Liao et al. 2008; Castro-Díez et al. 2014; Finerty et al. 2016; Jo et al. 2015b). Yet our study did find distinct relationships between native and non-native lianas and soil nutrient availability since we found no relationships between native lianas and soil processes for both the grouped and species-level data. Therefore, while data aggregated by native status fails to capture the magnitude and sign of species-level effects, origin is still a useful categorization for our system. Our findings also support management efforts that specifically target invasive, as opposed to native, lianas. What we do not uncover in our study is why the four different invasive liana species have dramatically different impacts on soil nutrient availability. Leaf trait differences offer one possible explanation. Traits of invasive species are often linked to increased resource acquisition rates (Leishman et al. 2007; van Kleunen et al. 2010; Ordonez et al. 2010). Further research comparing functional traits of co-occurring invasive lianas is needed to determine whether differences in leaf inputs are linked to changes in soil nutrient availability.

We acknowledge that the observational approach of this analysis limits our ability to determine causal relationships between lianas, forest disturbance, and C and N cycling. However, our approach does demonstrate how observational data—that may be more readily available to land managers through datasets like the NYC Ecological Assessment—can be used to inform management decisions under constrained budgets and limited resources (Sagarin and Pauchard 2010). Future experimental studies are still necessary to unambiguously determine whether invasive lianas directly change C and N availability. There is mounting evidence that urbanization and other factors of global change can promote the proliferation and spread of lianas in forested ecosystems worldwide (Phillips et al. 2002; Schnitzer and Bongers 2011; Brice et al. 2014; Laurance et al. 2014). Increased understanding of the impacts of lianas on soil processes will therefore improve our ability to predict changes to forested ecosystems in the face of global change. We found that while disturbance appears to promote the colonization of invasive lianas in forested ecosystems, lianas further alter C and N dynamics post-establishment. These changes may increase the resiliency of invaded ecosystems to restoration (Suding et al. 2004). Current management prescriptions in heavily invaded forests typically focus on invasive species removal. Although continuous and prolonged management of target invaders can shift the long-term trajectory of forest composition (Johnson and Handel 2016, 2019), these efforts may not restore other ecological processes that promote invasion. The linkages between soil processes and invasive liana cover observed in this study highlight the importance of considering plant-soil interactions to overcome barriers to restoration (Suding et al. 2004; Didham et al. 2005; Bauer 2012).

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Author contributions EBW, MAB and CCP designed the study. CCP designed and implemented the 2013–2014 citywide ecological assessment. EBW conducted the 2017 field and lab measurements. EBW, MAB, and SEK carried out the statistical analyses and contributed to data interpretation. EBW wrote the original manuscript, with contributions from all authors.

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