Forest canopy restoration has indirect effects on litter decomposition and no effect on denitrification

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Abstract.   Forest restoration has potential to recover degraded ecosystem functions in disturbed environments. Decomposition and denitrification are two critical functions involved in forest nutrient cycling that are often compromised in degraded ecosystems. As forest canopy structure develops following initial plantings, it may indirectly impact ecosystem functions by altering abiotic conditions. It is likely, however, that there are other abiotic factors that affect decomposition and denitrification that are unrelated to forest canopy structure. Here, we aimed to determine whether forest canopy openness, topography, and soil sand content would affect litter decomposition and denitrification by regulating the microclimate, the herbaceous plant layer, soil chemistry, and soil moisture. Research occurred in restored native temperate rainforest patches in two New Zealand cities. Urban forests are an excellent context for measuring impact of canopy restoration on ecosystem properties such as microclimate due to the extreme swings in city conditions (e.g., urban heat island). Decomposition rates were determined using leaf litter bags and denitrification rates through denitrification enzyme activity assays. We used structural equation modeling to quantify the direct and indirect drivers of these ecosystem functions. Results indicated that decomposition rates were positively related to soil moisture, relative humidity, and herbaceous plant cover. Interestingly, forest canopy openness indirectly affected decomposition through counteracting forces, meaning greater canopy openness in young forests permitted dense herbaceous plant growth which enhanced decomposition, while less canopy openness in older forests enhanced humidity levels which increased decomposition. Denitrification was negatively related to soil pH and positively related to soil moisture, but these abiotic factors were unrelated to the forest canopy. Discovering drivers of ecosystem functions can improve approaches to the restoration of degraded ecosystems, especially in disturbed urban areas. Identifying counteracting effects on ecosystem functions could improve management by focusing restoration actions on specific drivers to elicit desired changes. Some ecosystem processes, like denitrification, are not affected by forest canopy restoration or management, but are instead driven by edaphic and landscape factors.

Key words: counteracting effects; decomposition; denitrification; ecosystem function; forest restoration; structural equation modeling; urban ecology.

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Introduction

Our understanding of how restoration affects forest ecosystem function lags behind our understanding of how it impacts forest structure and composition (McKee and Faulkner 2000, Suding 2011, Wortley et al. 2013). It was once commonly assumed that the restoration of ecosystem structure and composition would lead to improved function, but this has been shown to be an oversimplification (Ehrenfeld and Toth 1997, Zedler and Callaway 1999, Ruiz-Jaen and Aide 2005,

Derhé et al. 2016). Moreover, in the studies where ecosystem processes have been evaluated following restoration, the specific mechanisms driving those processes are often not identified (Wortley et al. 2013). By pinpointing these mechanisms, we can improve the restoration of ecosystem functions (Guariguata and Ostertag 2001, Stanturf et al. 2014, Thackway and Freudenberger 2016). Here, we aimed to identify drivers of ecosystem functions involved with carbon and nutrient cycling in a heavily impacted ecosystem type: restored urban forest.

Soil carbon (C) and nitrogen (N) cycling are important forest ecosystem functions that involve many processes, including litter decomposition (Swift et al. 1979, Harmon et al. 1999), which is the return of C and N to the soil, and denitrification (Van der Heijden et al. 2008), which is the return of mineral N to the atmosphere through transformation into its gaseous form. Managing these ecosystem processes can be difficult because the rates at which decomposition and denitrification occur in restored urban forests are unique, unclear, and often driven by multiple factors (Pouyat et al. 1997, Reisinger et al. 2016).

An important driver contributing to altered C and N cycling in restored urban forests is forest canopy openness. Urban forest restoration in New Zealand often requires control of exotic deciduous tree species (e.g., *Salix* spp. and *Populus* spp.) in order to regain historically evergreen, closed forest canopies. A partially deciduous canopy likely changes nutrient cycling dynamics (Aerts and Berendse 1989) in two ways. First, the *en masse* annual leaf drop causes large swings in canopy openness and therefore increases sunlight and alters other abiotic conditions on the forest floor. Second, deciduous leaves generally break down faster than native evergreen species because of their lower lignin:N ratio (Cornwell et al. 2008), hence speeding the rate of decomposition and nutrient recycling. Even with removal of deciduous trees, newly planted forests are characterized by open canopies because of their small trees, and hence exhibit altered sunlight and abiotic conditions on the forest floor.

Another major driver of nutrient cycling in urban forests is nutrient pollution loads, which are generally most evident in urban forests as N runoff and deposition. This inflated N is known to alter urban forest composition by benefitting N-demanding exotic weed species (Gilliam 2006). Together, the forces of increased canopy openness and N pollution can shift the balance in favor of weeds that quell native tree regeneration (Maule et al. 1995, Wallace et al. 2017).

Urban forest is the ideal context to observe how abiotic properties affect nutrient cycling because of the extreme swings in abiotic conditions in cities. The high edge to interior ratio inherent to small urban forest patches negatively affects an array of properties, such as altered vegetation structure, increased sunlight availability, greater fluctuations in humidity, greater soil compactness, and more exposure to pollution (Matlack 1993, Young and Mitchell 1994, Murcia 1995, Harper et al. 2005, Malmivaara-Lämsä et al. 2008). Urban forests are therefore particularly disrupted by edge effects because of their small patch size and isolation, compounded by the altered environment of the surrounding urban matrix (e.g., asphalt causing the urban heat island; Oke et al. 1989). Further, these altered abiotic conditions pose a substantial challenge to urban land managers' increasing attempts to restore forest ecosystem functions, highlighting the importance of discovering which conditions to manage most carefully.

The main factors thought to control rates of litter decomposition include atmospheric relative humidity (Aerts 1997), the herbaceous plant layer (Standish et al. 2004, Ossola et al. 2016, Zirbel et al. 2017), and soil temperature and moisture (Vitousek et al. 1994, Pouyat et al. 1997, Cortez 1998, Sun and Zhao 2016). These factors can be indirectly controlled by forest canopy openness, landscape topography, and soil texture. Canopy openness is driven by increased tree basal area as restored forests age and is therefore a more direct driver of ecosystem processes than forest age itself (Wallace et al. 2017). Standish et al. (2004) found that decomposition rates of tree leaves doubled beneath mats of the herbaceous exotic weed *Tradescantia fluminensis* Vell., and this was attributed to a more favorable microclimate and habitat for the decomposer community.

Denitrification is the anaerobic process by which nitrate is converted by soil microbes to nitrogen gases, mainly N_2O and N_2 (Robertson and Groffman 2007). This conversion is instrumental in ameliorating N pollution, which is an environmental concern due to the vast quantities of N applied as

horticultural and agricultural fertilizer and produced by fossil fuel combustion (Vitousek et al. 1997, Galloway et al. 2003). Increased soil N may negatively impact plant communities (Prober and Wiehl 2011) by facilitating exotic weeds that outcompete regenerating native trees and causing long-term changes in forest composition. Increased N deposition also causes soil acidification (Tian and Niu 2015) that reduces plant growth and species diversity and can leach into groundwater and contaminate surface water bodies, causing eutrophication (Galloway et al. 2003, Hall et al. 2009). It is therefore crucial to determine drivers of denitrification in order to manage urban areas for excess nitrate removal.

The process of denitrification is controlled by the availabilities of oxygen, nitrate, and carbon (Knowles 1982). Therefore, a critical driver of denitrification is soil moisture (Klemedtsson et al. 1988, Robertson and Groffman 2007) because microbes will only use the denitrification process to produce energy in saturated conditions when oxygen is unavailable. Both soil C (Groffman et al. 1987, Barton et al. 1999, Robertson and Groffman 2007) and the mineral forms of N (Lowrance 1992, Robertson and Groffman 2007) are required for denitrification activity. Denitrifying microbes produce energy during reduction of NO_3^- with carbon compounds acting as electron donors. Soil pH is also known to govern denitrification, where denitrification is typically higher in alkaline soils (Šimek and Cooper 2002). Restoration of urban forest canopies could improve conditions for denitrification by increasing soil moisture as well as C inputs through production of evergreen leaves and other C-rich plant matter.

The objective of this study was to assess whether forest canopy structural development following restoration can affect two ecosystem functions related to C and N cycling: decomposition and denitrification. Here, we measured rates of leaf litter decomposition and denitrification in restored temperate urban forests and used structural equation modeling to determine which ecosystem properties most strongly regulated these processes. We asked (1) Is restoration of forest canopy structure related to decomposition and denitrification? and (2) What are the key direct and indirect drivers of decomposition and denitrification?

MATERIALS AND METHODS

Study sites

Our study took place on New Zealand's North Island, which was historically 75% covered in temperate rainforest but 66% of which is now cleared for agriculture and silviculture (Nicholls 1980). Data were collected from restored urban forest patches in two cities, Hamilton, population 160,000 (37.7870° S, 175.2793° E), and New Plymouth, population 60,000 (39.0556° S, 174.0752° E), about 200 km apart. Hamilton has an annual mean precipitation of 1110 mm with mean minimum and maximum temperatures of 8.7°C and 18.9°C, respectively (NIWA National Climate Database), and 2.1% indigenous forest cover (Clarkson et al. 2007b). New Plymouth has an annual mean precipitation of 1400 mm with mean minimum and maximum temperatures of 10°C and 17.5°C, respectively (NIWA National Climate Database), and 8.5% indigenous forest cover (Clarkson et al. 2007a) of a species composition similar to Hamilton. The restored urban forest patches used in this study averaged 2.05 ha (±1.6 ha SD) in size and were 159.7 m (±201.4 m SD) from any neighboring forest patch >0.1 ha.

Data were collected from restored urban forest patches (n = 27) aged from 3 to 70 years since initial planting (Appendix S1). These experimental sites were historically native evergreen rainforest, then converted to agriculture, and then planted with native tree seedlings generally directly into herbaceous exotic pasture. Further description of these restored forests is given in Wallace et al. (2017). Our experimental unit was the urban forest patch, and in order to capture heterogeneity, each forest patch encompassed three randomly located 10 × 10 m^2 plots, with constraints that plot edges were never <1 m from each other or the forest edge, or on slopes >10°. Five permanent 1-m^2 subplots were established in each of these plots (totaling 15 subplots per forest patch). No pseudoreplication occurred because values from plots and subplots were averaged, and analyses occurred at the forest patch level.

Data collection

Canopy openness was measured four times, once per season over a year (April 2014–May 2015) by taking hemispherical photographs of

the tree canopy from 1 m above the ground in each plot using a fish-eye lens. Resulting images were analyzed with the software Gap Light Analyzer v. 2.0 (Institute of Ecosystem Studies, Millbrook, New York, USA). The average value across the three plots and four seasons was used to quantify forest patch canopy openness, an index of sunlight availability. The forest floor herbaceous plant layer was assessed within the fifteen 1 m^2 subplots by estimating percent cover, which could exceed 100% due to plant overlap in three-dimensional space. The total area surveyed for herbaceous plant cover within each forest patch thus summed to 15 m^2.

We calculated a topographic index (McNab 1993) by standing in the central plot at each forest patch site and measuring the gradient, in percent, from the plot center to the horizon at eight equidistant compass directions, and computed the average gradient for each forest patch. Low topographic index values represent flat areas and ridges, whereas high values represent gullies.

Soil samples for assessing sand content, total C, and pH measurements were collected by removing leaf litter and coring to 15 cm in three subplots per plot. The resulting nine cores per site were homogenized, air dried, and analyzed. Prior to C analysis, samples were sieved (2-mm sieve), fine roots removed by hand, and samples finely ground with mortar and pestle. Soil C was determined using an Elementar vario EL cube (Elementar Analysensysteme GmbH, Langenselbold, Germany). Prior to particle size analysis to determine percent sand, silt, and clay, soil samples underwent hydrogen peroxide digestion to remove organic material and were processed with a Malvern Mastersizer 2000 (Malvern, UK). Soil pH samples were made into slurries (1:2 soil:water) followed by potentiometric determination (Blakemore et al. 1987). Only percent sand was used in the analysis because of its high drainage rate.

We measured nitrate (NO_3^-) twice (March and December 2015), because it is a labile form of N and levels fluctuate and calculated average nitrate concentrations in each forest patch. The coring protocol was the same as for sand content, C, and pH, except was only to 8 cm, and soil was kept refrigerated and moist until testing within 3 d. Nitrate was extracted with 2M KCl using a 1:10 soil:extractant ratio and a 1-hr end-over-end shake followed by filtration (Blakemore et al. 1987) and

determined by Cd reduction and NEDD colorimetry (Lachat Instruments 1998), both using a QuikChem 8500 flow injection analyzer (Lachat Instruments, Loveland, Colorado, USA).

Soil moisture was measured monthly for 12 mos in the center of each plot using a time domain water reflectometer probe (Hydrosense CS 620, Campbell Scientific, Logan, Utah, USA). Soil temperature at 10 cm depth was measured every four hours for 12 mos in the center subplot in two of the plots at each forest patch using thermochrons (iButton dataloggers model DS1921G-F5; Maxim Integrated, San Jose, California, USA; Hubbart et al. 2005). Atmospheric relative humidity was measured every four hours for 12 mos using hygrochrons (iButton dataloggers model DS1923, Maxim Integrated, San Jose, California, USA). Hygrochrons (one/forest patch) were hung in radiation shields 2 m above the center of the central plot. For soil moisture, temperature, and the relative humidity, we computed the mean over one year to represent these conditions at each forest patch.

Decomposition rates in forest patches were quantified using the leaf litter bag method (Bocock and Gilbert 1957, Wieder and Lang 1982, Harmon et al. 1999). Litter bags were 20 × 20 cm in size and constructed of coarse and fine mesh types of UV-resistant high-density polyethylene shadecloth (Cosio Industries, Auckland, New Zealand). The coarse side (1 × 2 mm pores) was placed skywards, and the finer shadecloth (<1 mm pore size) rested on the ground. Larger pores provide access for meso/macrofauna, and smaller pores prevented loss of small leaf pieces. Litterbags were stitched with nylon thread (Bocock and Gilbert 1957, Harmon et al. 1999) and filled with leaves of *Beilschmiedia tawa*, a native tree species chosen as a standard material for use in all restored forest patches to determine the potential decomposition rates.

Beilschmiedia tawa was once an important, dominant canopy species of native forests in the study region but is now relatively rare. *Beilschmiedia tawa* was not present in the restored forest plots except for one, where it represented only 0.23% of basal area. This ensured that a specialist decomposer community adapted to specifically *B. tawa* leaves was unlikely to be present. Naturally senesced, recently dropped *B. tawa* leaves were collected by hand and oven-dried at 60°C

for one week, and approximately 5 g of leaves was placed in each litter bag to mimic naturally occurring leaf litter densities.

Litterbags were closed with stainless steel staples. Three litter bags were placed in each plot, totaling nine litter bags per forest patch. Litterbags were secured to the forest floor with stainless steel pegs, placed so they mimicked natural litter fall, and retrieved after 14 mos and contents cleaned of soil. Litter was oven-dried at 60°C for one week and weighed. Proportion mass loss was calculated for each bag, and an average of the nine bags per restored forest patch was computed. The decomposition measurements were only taken in Hamilton (n = 17).

Microbial denitrification potential in the forest soils was ascertained through denitrification enzyme activity (DEA) assays using the acetylene inhibition method (Groffman et al. 2006) under optimal conditions in anoxic N- and C-amended slurries (Bruesewitz et al. 2011). A DEA assay estimates the capacity of denitrifying enzymes in soil microbes to convert nitrate into the gaseous forms of N at the time of sampling. Acetylene is used to inhibit the usual reduction of N_2O to N_2 and allows quantification of denitrification following measurement of N_2O. Soil collection and DEA assays were conducted in March 2015 (NZ late summer). The full protocol is detailed in Appendix S2.

Statistical analyses

Relationships between ecosystem structure and function.—We inspected bivariate relationships and fitted generalized linear regression models with the identity link function and Gaussian error distributions to evaluate the relationships between either decomposition or denitrification and ecosystem attributes that we hypothesized were indirectly or directly related to these individual functions (Fig. 1), as well as forest age (years since planting). Analyses were conducted at the forest patch level. Prior to analysis, all variables except forest age, sand, pH, and soil moisture were log transformed to linearize relationships. Topographic index was square root transformed. All variables were scaled to unit variance. No variables exhibited multicollinearity because all variance inflation factors (VIF) were close to one. Analysis was performed using the statistical software R version 3.4.3.
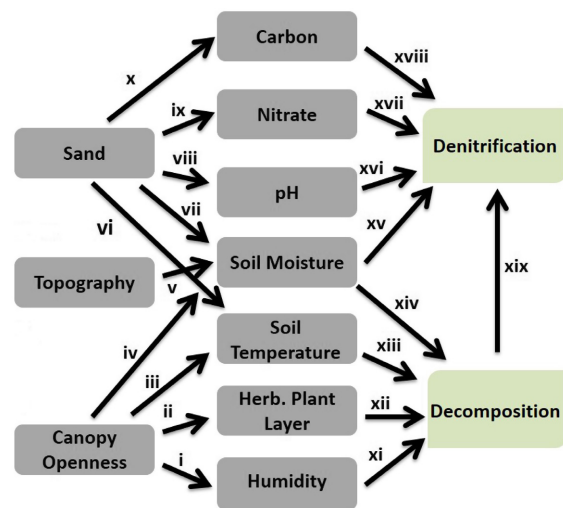

Fig. 1. Hypothesized a priori structural equation model illustrating how properties of restored forests might influence litter decomposition and denitrification. The functions are light green, and their hypothesized drivers are dark gray. Model fit was assessed using Fisher's C statistic (Lefcheck 2015), where good-fitting models yield small C statistics and P-values >0.05. This a priori structural equation model of decomposition and denitrification did not fit the data well (Fisher's C = 136.56, df = 88, P = 0.001). Supporting references for causal relationships are listed by pathway number: (i) McCune and Antos 1982, (ii) McAlpine et al. 2015, (iii) Chen et al. 1993, (iv) Gray et al. 2002, (v) Nyberg 1996, (vi) Bowers and Hanks 1965, (vii) Clapp and Hornberger 1978, (viii) Gray et al. 1998, Voroney 2007, (ix) Robertson and Groffman 2007, Hansen and Djurhuus 1996, (x) Gregorich et al. 1989, (xi) Aerts 1997, (xii) Ossola et al. 2016, Standish et al. 2004, (xiii) Cortez 1998, Pouyat et al. 1997, (xiv) Cortez 1998, Sun and Zhao 2016, Vitousek et al. 1994, (xv) Robertson and Groffman 2007, Klemedtsson et al. 1988, (xvi) Šimek and Cooper 2002, (xvii) Robertson and Groffman 2007, Lowrance 1992, (xviii) Robertson and Groffman 2007, Groffman et al. 1987, Barton et al. 1999, (xix) Schipper et al. 1994.

Drivers of decomposition and denitrification.—We used structural equation modeling with the R package piecewiseSEM (Lefcheck 2015) to determine the direct and indirect drivers of decomposition and denitrification. This multivariate approach tests hypothesized relationships among a system of state variables. Using

support from the primary literature, we developed an a priori model that we believed to be the most plausible causal structure of the factors driving decomposition and denitrification in restored forests (Fig. 1).

In this a priori model, we hypothesized that decreased canopy openness (Wallace et al. 2017) would indirectly increase litter decomposition by creating greater soil moisture conditions (Vitousek et al. 1994, Cortez 1998, Gray et al. 2002), cooler soil temperatures (Chen et al. 1993, Cortez 1998, Wallace et al. 2017), and higher relative humidity (McCune and Antos 1982, Aerts 1997, Wallace et al. 2017) as well as suppressing the herbaceous plant layer (Standish 2004, McAlpine et al. 2015, Wallace et al. 2017).

We also hypothesized that soil sand content and topography would indirectly control decomposition and denitrification. We predicted increased sand content would indirectly affect decomposition by decreasing the soil temperature (Bowers and Hanks 1965) and decreasing both decomposition and denitrification rates by decreasing soil moisture (Clapp and Hornberger 1978, Groffman et al. 1987, Groffman and Tiedje 1989, Zirbel et al. 2017). We predicted denitrification rates to increase in greater soil moisture conditions within gully landscapes (Nyberg 1996). We also predicted that higher soil sand content would indirectly reduce denitrification because of greater N loss through nitrate leaching (Lowrance 1992, Hansen and Djurhuus 1996, Robertson and Groffman 2007), and decreased C availability (Groffman et al. 1987, Gregorich et al. 1989, Robertson and Groffman 2007). Soil sand content can have varying effects on soil pH depending on the study system, but we expected that denitrification rates would be higher in alkaline soils (Gray et al. 1998, Šimek and Cooper 2002, Voroney 2007). Finally, we predicted that fast decomposition rates would be positively associated with high rates of denitrification (Schipper et al. 1994).

Model fit was assessed using Fisher's C statistic (Lefcheck 2015), where good-fitting models yield small C statistics and P-values >0.05. Poor fitting models were improved by removing nonsignificant pathways and variables that were not significantly related to the response variables ($\alpha = 0.05$).

RESULTS

Relationships between ecosystem structure and function

Bivariate relationships revealed that decomposition had a direct, significant, positive relationship with two ecosystem properties: soil moisture ($R^2 = 0.40$, $P = 0.006$, Fig. 2A) and herbaceous plant layer cover ($R^2 = 0.32$, $P = 0.018$, Fig. 2B), and no other variables (Fig. 2C–H). Denitrification was significantly related to four of the properties we investigated: Soil moisture was positively correlated with denitrification ($R^2 = 0.59$, $P < 0.001$, Fig. 3A), whereas soil pH was negatively correlated with denitrification ($R^2 = 0.32$, $P = 0.002$, Fig. 3B). Denitrification was associated with decreased soil sand content ($R^2 = 0.24$, $P = 0.009$, Fig. 3C), and increased soil C ($R^2 = 0.23$, $P = 0.011$, Fig. 3D), but no other variables (Fig. 3E–H).

Drivers of decomposition and denitrification

The a priori structural equation model of decomposition and denitrification did not fit the data well (Fisher's $C = 136.56$, df $= 88$, $P = 0.001$; Fig. 1). We removed the nonsignificant pathways from decomposition to denitrification and from canopy openness to soil moisture (pathways xix and iv, respectively, Fig. 1) and removed soil temperature, C, and nitrate from the model because they did not explain significant variation in any response (despite some significant bivariate relationships, Fig. 3). This new model fit the data well and explained significant variation in decomposition (74%) and denitrification (70%). The final model also explained significant variation in the herbaceous plant layer (31%), humidity (36%), soil moisture (38%), and soil pH (47%; Fig. 4). The final model indicated that decomposition was highest under greater herbaceous plant layer cover, higher humidity, and greater soil moisture (Fig. 4).

Forest canopy structure (i.e., canopy openness) had no effect on denitrification. Instead, denitrification was controlled by abiotic properties and was highest when soil moisture was highest and pH lowest. Soil sand content increased soil pH and decreased soil moisture, and large topographic index scores (gully landscapes) increased soil moisture (Fig. 4).
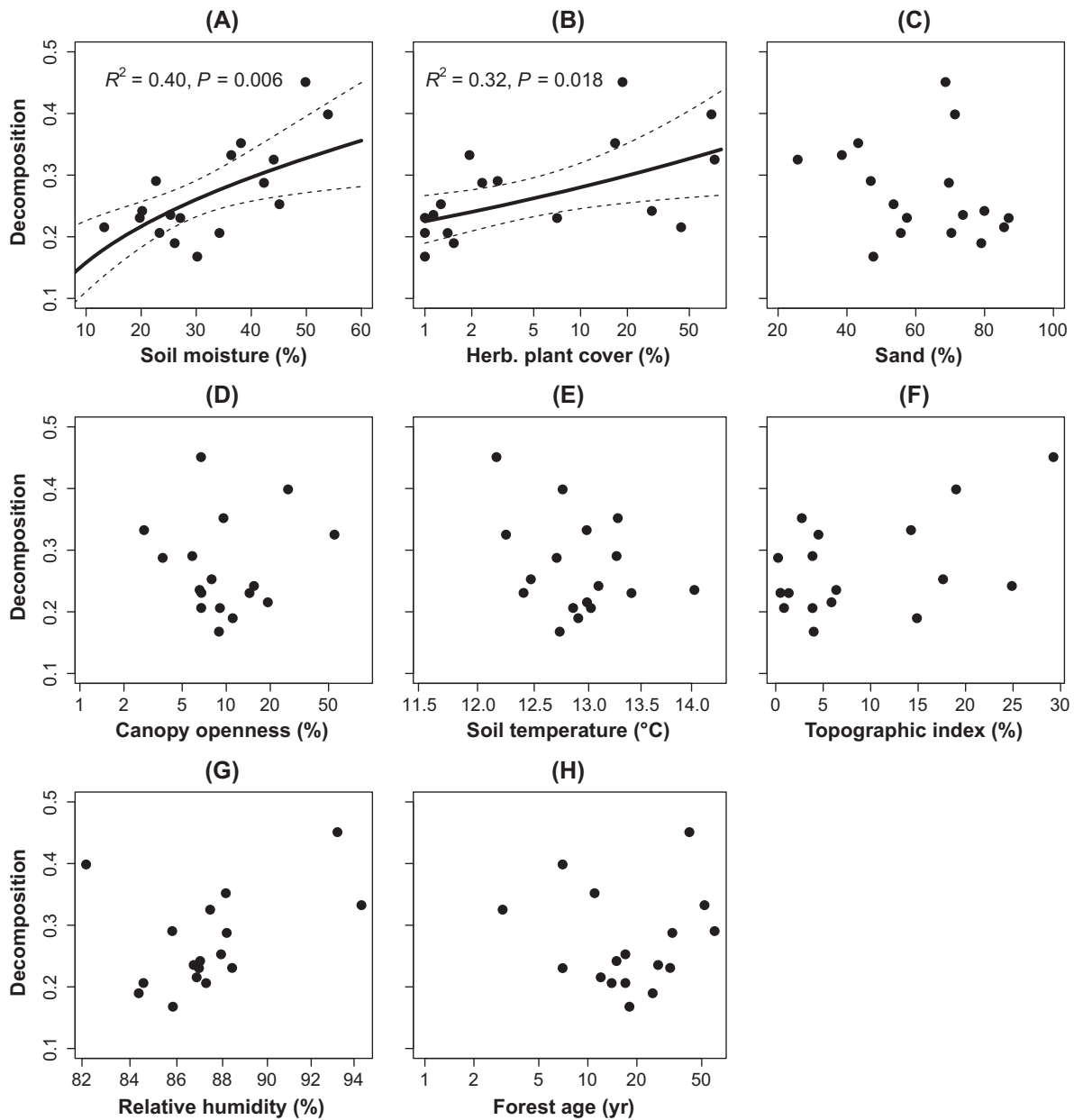
Fig. 2. Bivariate relationships between litter decomposition (proportion of mass loss) and restored forest ecosystem properties. Points represent restored forests. Litter decomposition rates were only monitored in Hamilton (n = 17). Significant relationships are shown with solid lines representing the fitted values from a linear regression model, with dashed lines representing 95% confidence intervals. Ecosystem property values shown on the x-axis are displayed log scale if they were log transformed for the structural equation model (including herbaceous plant cover, canopy openness, soil temperature, and relative humidity), but otherwise are not transformed.
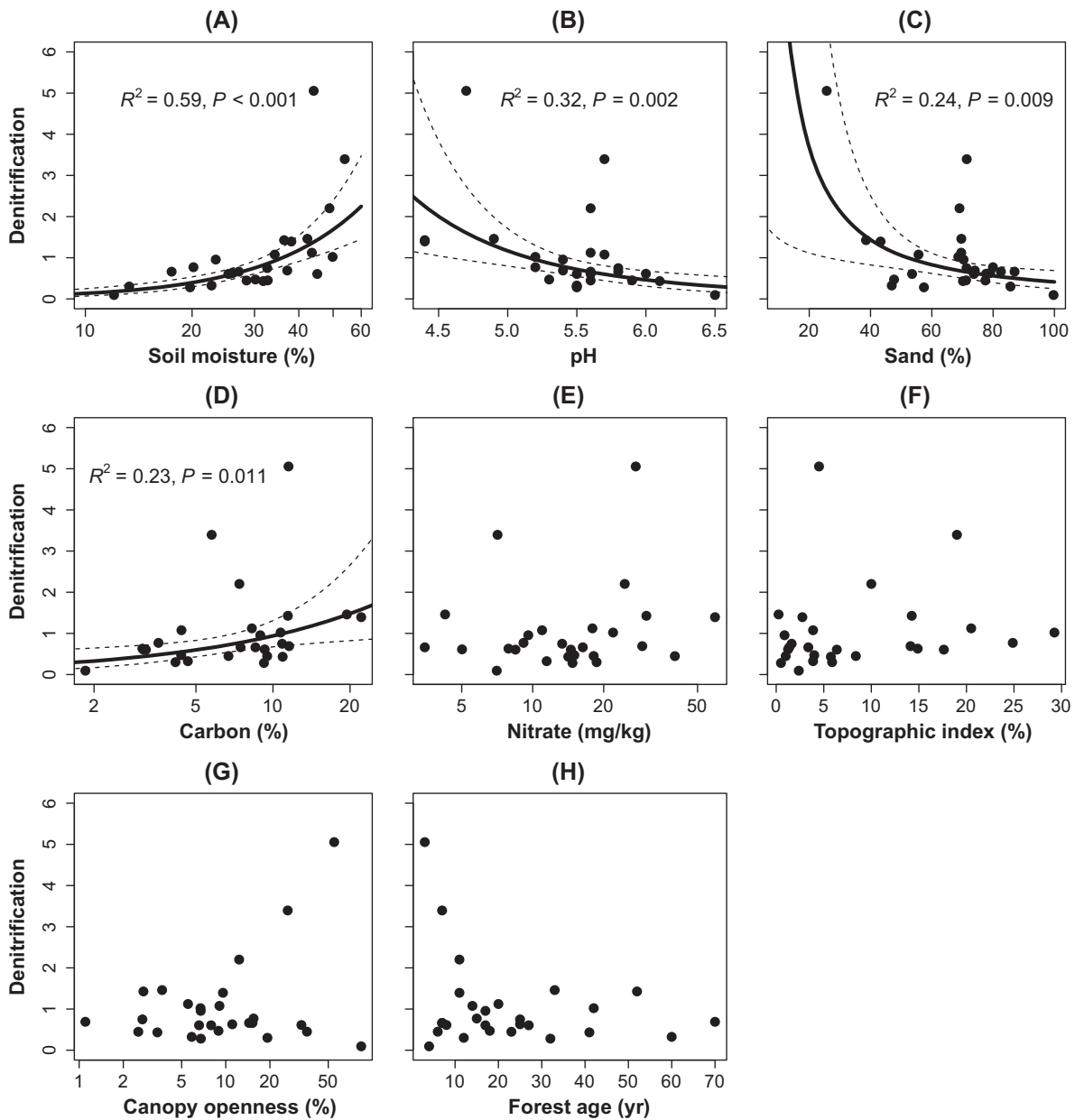
Fig. 3. Bivariate relationships between denitrification potential (μg $N_2O \cdot h^{-1} \cdot [g$ $soil]^{-1}$) and restored forest ecosystem properties. Points represent restored forests ($n = 27$). Significant relationships are shown with solid lines representing the fitted values from a linear regression model, with dashed lines representing 95% confidence intervals. Ecosystem property values shown on the x-axis are displayed log scale if they were log transformed for the structural equation model (including carbon, nitrate, and canopy openness), but otherwise are not transformed.

Discussion

Restoration studies too often focus exclusively on either plant community structure or diversity, without considering functional processes (Montoya et al. 2012). Results presented here expand our understanding of functional processes in restored forests. They indicate that forest canopy structure and abiotic landscape properties can control litter decomposition and
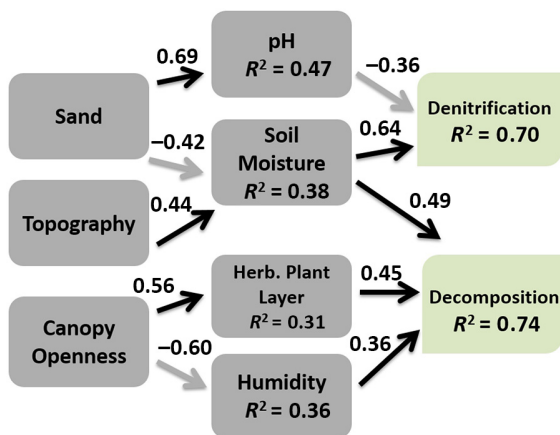
Fig. 4. The final structural equation model, illustrating drivers of decomposition ($n = 17$) and denitrification ($n = 27$). The ecosystem functions of decomposition and denitrification are shown in light green, and their drivers are shown in dark gray. Values by arrows are standardized path coefficients. R^2 values are shown in the box of each response variable. For clarity, positive pathways are black and negative pathways are gray. Model fit was assessed using Fisher's C statistic (Lefcheck 2015), where good-fitting models yield small C statistics and P-values >0.05. This model fit the data well (Fisher's $C = 59.96$, df = 46, $P = 0.081$). Two counteracting indirect relationships linking canopy openness and decomposition are mediated through the herbaceous plant layer (a positive relationship) and humidity (a negative relationship).

denitrification, two critical steps in the cycling of C and N. We observed that the forest canopy indirectly exerted counteracting direct effects on decomposition, while denitrification was independent of forest canopy and was instead driven indirectly by topography and soil texture. Specifically, decomposition was directly driven by soil moisture, the herbaceous plant layer, and relative humidity, while denitrification was driven by soil pH and soil moisture. Importantly, the structural equation model illustrated that indirect drivers of ecosystem functions are not always apparent from bivariate relationships when they are mediating counteracting direct effects.

Counteracting effects occur when one driving variable causes simultaneous results in two response variables such that their effects on a third variable are essentially canceled out. Counteracting indirect effects likely occur often in

ecosystems, but it can be difficult to identify without an appropriate multivariate analysis (Grace et al. 2010). Bivariate regression analyses alone can be misleading and cause researchers and managers to disregard important ultimate causal forces. Using regression analyses, Hall et al. (2009) found that fractions of agricultural and urban land predicted nitrate uptake in streams, but further analysis using structural equation modeling revealed that land use was the indirect driver of nitrate uptake, mediated by the counteracting forces of nitrate concentration and gross primary production.

Interestingly, in our model, forest structure (i.e., canopy openness) did have strong indirect effects on decomposition, but the simple bivariate relationship between canopy openness and decomposition was not significant. This was because canopy openness had counteracting indirect effects on decomposition that were mediated through the herbaceous plant layer and humidity. Herbaceous plant cover and humidity both increase decomposition, but canopy closure leads to suppression of herbaceous plants and an increase in humidity. Therefore, these direct effects counteracted one other. Revealing these complex relationships through multivariate modeling can improve management practices by targeting the specific direct effects that influence an ecosystem function, rather than focusing on less-proximate indirect drivers.

When the forest canopy is young and open, the flourishing herbaceous plant layer fosters decomposition, perhaps because it provides structural habitat and suitable microclimate for decomposers (Standish et al. 2004). As forest canopy cover increases and blocks sunlight, herbaceous plant cover declines. Concurrently, humidity levels increase and stabilize (Wallace et al. 2017), also increasing decomposition rates. Therefore, the indirect effects of canopy cover on decomposition are mediated through these counteracting effects, such that the total net effect is null. In terms of management, this implies that decomposition rates can be slowed if herbaceous weeds are removed beneath developing forest canopies. Indeed, exotic weed management is common practice in the first few years of a restoration project to stifle competition with plantings.

Exotic deciduous woody species could also alter decomposition dynamics (Vivanco and

Austin 2008, Trammell et al. 2012) by producing pulsed inputs of leaf litter and seasonal swings in solar radiation that cause humidity fluctuations (Wallace et al. 2017) and a permanent herbaceous layer. This is concerning as the herbaceous layer in New Zealand forests is primarily exotic and could have long-term negative impacts on soil properties (Peltzer et al. 2009) and forest regeneration (Standish et al. 2001, Davis et al. 2005) if allowed to persist. Zirbel et al. (2017) found that in prairie restoration both plant trait composition and environmental conditions predicted ecosystem functioning, with variation in which plant traits affected which functions (Suding et al. 2008). This suggests that a transition from a native forest trait composition to one of exotic plant traits could also result in altered ecosystem functioning. Our data indicate that young, open, forest canopies facilitate accelerated decomposition rates because these sunny conditions promote an exotic herbaceous plant layer in which exotic, deciduous litter could more easily be broken down than tougher native evergreen leaves. Litter decomposition rates can control the speed of tree seed germination and establishment (Xiong and Nilsson 1999). By understanding factors such as what plant community traits and environmental conditions control decomposition, we will better predict future forest composition.

Forests undergoing restoration will exhibit structural change that manifests as a newly closed canopy followed by a subsequent decline of the herbaceous plant layer that affects much of the ecosystem. In maturing evergreen forests, a transition in the specialist decomposer community can occur when herbaceous plants senesce, and instead, ligneous, evergreen tree detritus accumulates on the forest floor (Gartner and Cardon 2004). Further structural changes after herbaceous plant decline will include the regeneration of native tree species in the understory (Wallace et al. 2017).

Denitrification was not driven by forest structure but instead by the indirect abiotic controls of soil sand content and topography. Sand content regulated two direct drivers of denitrification: soil moisture and soil pH. As expected, soil moisture was lower in soils with high sand content because they have lower water holding capacity (Groffman and Tiedje 1989, Barton et al. 1999).

The negative relationship between soil pH and denitrification was unexpected, probably because the relationship between pH and denitrification is not well understood and likely has many mediating factors that we did not measure (Šimek et al. 2002). For example, ample availability of C and N can enable high denitrification rates to occur regardless of pH, or sometimes, denitrifying bacteria adapt to slightly acidic conditions (Šimek et al. 2002). Topography was an indirect driver of denitrification because it determines drainage patterns. Gullies retain higher soil moisture than hilltops. Our results identify the major influence that edaphic conditions have on denitrification, something that should be considered on a landscape scale when making management decisions (Groffman and Tiedje 1989, Quesada et al. 2012). Generally, results indicate that abiotic landscape properties can exert stronger control over some ecosystem processes than vegetation manipulation.

Conclusions

In summary, our model suggests that restoration of forest canopy structure has counteracting indirect effects on decomposition, but no effect on denitrification. We expected that a closed canopy would foster moist soil conditions which drive higher denitrification by preventing evaporation through solar irradiation, but our results illustrate that establishing canopy cover cannot be used as a technique for increasing denitrification. Instead, denitrification is influenced by local abiotic factors and large-scale drainage patterns. To counter the excess nitrogen resulting from anthropogenic activities, we recommend setting aside or engineering landscape features where denitrification can occur, for example, low-lying areas with fine soil textures such as gullies and wetlands or bioreactors (Long et al. 2011). Such a targeted approach will allow imbalances in nutrient cycling to be addressed with success and emphasizes how specific ecosystem functions can be produced only by the appropriate landscape type.

Land managers and policy makers should recognize that a range of ecosystems must be protected or restored to provide various ecosystem functions, but knowing which areas to protect or restore can only be determined by linking specific properties to the desired function. Our results

demonstrate that this is possible, and further, by using structural equation modeling we can uncover direct and indirect drivers and potentially counteracting effects on ecosystem functions.

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